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Shrimps of the genus *Periclimenes* (Crustacea, Decapoda, Palaemonidae) associated with mushroom corals (Scleractinia, Fungiidae): linking DNA barcodes to morphology

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Abstract

Most marine palaemonid shrimp species live in symbiosis with invertebrates of various phyla. These associations range from weak epibiosis to obligatory endosymbiosis and from restricted commensalism to semi-parasitism. On coral reefs, such symbiotic shrimps can contribute to the associated biodiversity of reef corals. Among the host taxa, mushroom corals (Cnidaria: Anthozoa: Fungiidae) are known to harbour various groups of symbionts, including shrimps. Some but not all of these associated species are host-specific. Because data on the host specificity of shrimps on mushroom corals are scarce, shrimp species of the genus *Periclimenes* were collected from mushroom corals during fieldwork in Lembeh Strait,

North Sulawesi, Indonesia. Using molecular (COI barcoding gene) and morphological methods, three species of *Periclimenes* were identified: *P. diversipes*, *P. watamuae* and a species new to science, *P. subcorallum* sp. nov., described herein. Their host specificity was variable, with eight, three and two fungiid host records, respectively. It is concluded that shrimp species of the genus *Periclimenes* show much overlap in their host choice and that particular morphological traits in the host species appear to play a more important role than phylogenetic affinities within the host group.

Keywords

Caridea – Fungiidae – host corals – Indo-Pacific – new species – North Sulawesi – Scleractinia – taxonomy

Zoobank: <http://zoobank.org/urn:lsid:zoobank.org:pub:C34DC191-0357-4D14-BB42-D69F29E5657B>

1 Introduction

The large majority of marine palaemonid shrimp species live in symbiosis with invertebrates of various phyla. These associations range from weak epibiosis to obligatory endosymbiosis and from restricted commensalism to semi-parasitism, with the specialisation to particular hosts likely playing a role in the diversification of this shrimp group (Horká et al., 2016). These associated shrimps species contribute to the biodiversity of coral reefs although they cannot always be found very easily (Hoeksema, 2017).

Scleractinian corals are well known as possible host species for symbiotic shrimps of the family Palaemonidae, both in the Caribbean and the Indo-Pacific. Examples are found among shrimp species of the genera *Anapontonia* Bruce, 1966, *Ancylocaris* Schenkel, 1902, *Ancylomenes* Okuno & Bruce, 2010, *Coralliocaris* Stimpson, 1860, *Ctenopontonia* Bruce, 1979, *Cuapetes* Clark, 1919, *Fennera* Holthuis, 1951, *Hamodactylus* Holthuis, 1952, *Hamopontonia* Bruce, 1970, *Harpiliopsis* Borradaile, 1917, *Harpilius* Dana, 1852, *Ischnopontonia* Bruce, 1966, *Izucaris* Okuno, 1999, *Jocaste* Holthuis, 1952, *Metapontonia* Bruce, 1967, *Paratypton* Bals, 1914, *Periclimenes* O.G. Costa, 1844, *Philarius*

Holthuis, 1952, *Platycaris* Holthuis, 1952, *Pliopontonia* Bruce, 1973a, *Pontonides* Borradaile, 1917 *Tectopontonia* Bruce, 1973b, *Vir* Holthuis, 1952, and *Yemenicaris* Bruce, 1997 (Fransen, 1989, 1997; Fransen & Holthuis, 2007; Okuno, 2009; De Grave & Fransen, 2011; Fransen & Rauch, 2013; Brinkmann & Fransen, 2016; Horká et al., 2016; Ďuriš & Lin, 2017). Among the scleractinian hosts, mushroom corals (Scleractinia: Fungiidae) are also known to harbour various groups of symbionts, including shrimps (De Grave, 1998; Hoeksema & Fransen, 2011; Hoeksema et al., 2012; Fransen & Rauch, 2013). Four of these shrimp species belong to the genus *Periclimenes* Costa, 1844 (Palaemonidae): *P. diversipes* Kemp, 1922; *P. goniopora* Bruce, 1989; *P. jugalis* Holthuis, 1952; and *P. watamuae* Bruce, 1976a (Hoeksema et al., 2012), which are all members of the *P. diversipes* species group designated by Bruce (1989). This group also includes some species observed in association with other stony corals (*P. difficilis* Bruce, 1976b; *P. madreporae* Bruce, 1969; *P. mahei* Bruce, 1969), soft corals (*P. kemp* Bruce, 1969), or sponges (*P. poriphilus* Bruce, 2010), although *P. difficilis* probably does not belong here as it has a linguiform median plate on the 4th thoracic sternite, which is lacking in other members of the group (Bruce, 2010).

Data on the host specificity of *Periclimenes* symbionts with regards to mushroom corals are scarce (Hoeksema et al., 2012). *Periclimenes diversipes* has been recorded from *Ctenactis crassa* (Dana, 1846) (Hoeksema et al., 2012) and *Herpolitha limax* (Esper, 1797) (Bruce & Coombes, 1995). This species however, has also been recorded as a symbiont of a wide range of other scleractinian corals (Fransen, 1997). *Periclimenes goniopora* has been recorded from the fungiids *Ctenactis echinata* (Pallas, 1766), *Fungia fungites* (Linnaeus, 1758), *Lithophyllon repanda* (Dana, 1846), and *Sandalolitha robusta* (Quelch, 1886) (Hoeksema et al., 2012), but is also known from other scleractinians (Fransen, 1997). *Periclimenes jugalis* is a very rare species recorded from the mushroom coral *Heliofungia actiniformis* (Quoy & Gaimard, 1833) (Hoeksema et al., 2012) but is otherwise only known from alcyonacean octocorals (Fransen, 1997). *Periclimenes watamuae* has been found in association with the fungiids *Halomitra pileus* (Linnaeus, 1758), *Heliofungia actiniformis*, *Herpolitha limax*, and *Polyphyllia talpina* (Lamarck, 1801) (Hoeksema et al., 2012) and is further known as a symbiont of other Scleractinia, and also of Alcyonacea (De Grave, 2000).

A faunal survey for shallow-water palaemonid shrimps associated with mushroom corals (Scleractinia: Fungiidae) during fieldwork near Lembeh Island, NE Sulawesi, Indonesia revealed three species of *Periclimenes*: *P. diversipes*, *P. watamuae* and a species new to science, *P. subcorallum* sp. nov., described herein (authored by Fransen & Rauch). Most specimens were found on the underside of free-living mushroom corals, including several that constitute new host records. As the name, *Periclimenes diversipes*, indicates, the chelipeds of this species are morphologically diverse, which is in part related to sex and size. To a lesser extent this also counts for *P. watamuae*. Distinguishing between especially small specimens of these two species

can be difficult because of their variability in cheliped shape. By sequencing cytochrome c oxidase I (COI) of multiple specimens with different sex and size from both species we aim to define several morphological and colour characters on which the two species can be distinguished.

Finally, we want to examine whether the *Periclimenes* species of the present study and congeneric species recorded from mushroom corals in previous studies show a host-specific relation, and whether this relation reflects the host group phylogeny or particular morphological traits in the host group, such as attached vs. free-living mode of life (Hoeksema, 1989; Gittenberger et al., 2011; Benzoni et al., 2012) and the maximum recorded corallum size (Hoeksema, 1991; Gittenberger et al., 2011).

2 Material and methods

2.1 Sample collection

Specimens were collected with the help of SCUBA during a Marine Biodiversity Workshop organized in February 2012 at the Bitung field station of the Research Centre of Oceanography (PPO-LIPI). Each shrimp was photographed and then captured in a plastic bag together with its host coral and taken to the lab for examination. After identification by the second author, the host corals were returned to the field. Shrimp specimens were photographed and preserved in 95% ethanol and their postorbital carapace length (pocl.) was measured. Data for all specimens studied are listed (table 1). Tissue samples from eggs or pleopods, were preserved in 95% ethanol before DNA extraction. Specimens are stored in the Crustacea collection of Naturalis Biodiversity Center (RMNH.CRUS.) Leiden, the Netherlands (formerly known as Rijksmuseum van Natuurlijke Historie) and the Museum Zoologicum Bogoriense, Research Center

TABLE 1 Taxa sampled for molecular and morphological analyses with reference to collection registration numbers of voucher specimens, location data, host, and GenBank accession numbers. *Sequences obtained from GenBank.

Species	Voucher	specimens	Locality	Host	GenBank accession No.
<i>Per. diversipes</i>	RMNH.CRUS.D.57543	1m.	Indonesia, Lembbeh Strait, LEM.05	Fungiidae: <i>Herpolitha limax</i>	MK843292
	RMNH.CRUS.D.57544	2fov., 3juv.	Indonesia, Lembbeh Strait, LEM.06	Fungiidae: <i>Danafungia scruposa</i>	MK843285
	RMNH.CRUS.D.57545	1f.	Indonesia, Lembbeh Strait, LEM.06	Fungiidae: <i>Heliogungia actiniformis</i>	MK843277
	RMNH.CRUS.D.57546	4m., 1f., 1fov., 1juv.	Indonesia, Lembbeh Strait, LEM.07	Fungiidae: <i>Danafungia scruposa</i>	MK843276
	RMNH.CRUS.D.57547	3m., 3fov., 1juv.	Indonesia, Lembbeh Strait, LEM.07	Fungiidae: <i>Lithophyllon repanda</i>	MK843284
	RMNH.CRUS.D.57548	2f.	Indonesia, Lembbeh Strait, LEM.07	Fungiidae: <i>Lithophyllon repanda</i>	MK843295
	RMNH.CRUS.D.57549	7juv.	Indonesia, Lembbeh Strait, LEM.08	Fungiidae: <i>Lithophyllon repanda</i>	MK843286
	RMNH.CRUS.D.57550	1juv.	Indonesia, Lembbeh Strait, LEM.09	Fungiidae: <i>Heliogungia actiniformis</i>	MK843287
	RMNH.CRUS.D.57551	1m., 1fov., 1juv.	Indonesia, Lembbeh Strait, LEM.11	Fungiidae: <i>Herpolitha limax</i>	MK843282
	RMNH.CRUS.D.57552	1fov.	Indonesia, Lembbeh Strait, LEM.12	Fungiidae: <i>Danafungia scruposa</i>	MK843294
	RMNH.CRUS.D.57553	1m.	Indonesia, Lembbeh Strait, LEM.14	Fungiidae: <i>Herpolitha limax</i>	MK843283
	RMNH.CRUS.D.57554	10m., 3fov., 7juv.	Indonesia, Lembbeh Strait, LEM.18	Fungiidae: <i>Sandalolitha robusta</i>	
	RMNH.CRUS.D.57555	1fov., 1juv.	Indonesia, Lembbeh Strait, LEM.19	Fungiidae: <i>Fungia fungites</i>	MK843290
	RMNH.CRUS.D.57556	2m., 1fov.	Indonesia, Lembbeh Strait, LEM.19	Fungiidae: <i>Lithophyllon repanda</i>	MK843279
	RMNH.CRUS.D.57557	3m., 1juv.	Indonesia, Lembbeh Strait, LEM.19	Fungiidae: <i>Lobactis scutaria</i>	MK843288
	RMNH.CRUS.D.57558	1fov.	Indonesia, Lembbeh Strait, LEM.20	Fungiidae: <i>Heliogungia actiniformis</i>	MK843278
	RMNH.CRUS.D.57559	1m., 1f., 2fov.	Indonesia, Lembbeh Strait, LEM.20	Fungiidae: <i>Danafungia scruposa</i>	MK843280
	RMNH.CRUS.D.57560	1f.	Indonesia, Lembbeh Strait, LEM.21	Fungiidae: <i>Ctenactis crassa</i>	MK843289
	RMNH.CRUS.D.57561	2f.	Indonesia, Lembbeh Strait, LEM.21	Fungiidae: <i>Ctenactis crassa</i>	MK843281
	RMNH.CRUS.D.57562	6m., 4fov., 7juv.	Indonesia, Lembbeh Strait, LEM.21	Fungiidae: <i>Sandalolitha robusta</i>	
	RMNH.CRUS.D.57563	1m., 1f., 1fov.	Indonesia, Lembbeh Strait, LEM.27	Fungiidae: <i>Danafungia scruposa</i>	
	RMNH.CRUS.D.57564	1m.	Indonesia, Lembbeh Strait, LEM.33	Fungiidae: <i>Lithophyllon repanda</i>	MK843293
	RMNH.CRUS.D.57565	1fov.	Indonesia, Lembbeh Strait, LEM.36	Fungiidae: <i>Lithophyllon concinna</i>	MK843291

<i>Per. watamuae</i>	RMNH.CRUS.D.30945	f. holotype, m. allotype	Kenya, Watamu	Alcyonaria: unidentified
	RMNH.CRUS.D.57566	1f., 1juv.	Indonesia, Lembbeh Strait, LEM.06	Fungiidae: <i>Herpolitha limax</i>
	RMNH.CRUS.D.57567	1m.	Indonesia, Lembbeh Strait, LEM.12	Fungiidae: <i>Danafungia horrida</i>
	RMNH.CRUS.D.57568	2m., 1fov.	Indonesia, Lembbeh Strait, LEM.23	Fungiidae: <i>Ctenactis crassa</i>
	RMNH.CRUS.D.57569	1m., 2juv.	Indonesia, Lembbeh Strait, LEM.23	Fungiidae: <i>Pleuractis gravis</i>
	RMNH.CRUS.D.57570	1fov., 2juv.	Indonesia, Lembbeh Strait, LEM.23	Fungiidae: <i>Ctenactis echinata</i>
	RMNH.CRUS.D.57571	1m., 1f.	Indonesia, Lembbeh Strait, LEM.25	Fungiidae: <i>Danafungia scruposa</i>
	RMNH.CRUS.D.57572	1juv.	Indonesia, Lembbeh Strait, LEM.26	Fungiidae: <i>Heliofungia actiniformis</i>
	RMNH.CRUS.D.57573	3m., 1fov., 3juv.	Indonesia, Lembbeh Strait, LEM.35	Fungiidae: <i>Danafungia horrida</i>
	RMNH.CRUS.D.57574	5m., 1f., 2fov., 1juv.	Indonesia, Lembbeh Strait, LEM.36	Fungiidae: <i>Pleuractis gravis</i>
<i>Per. subcorallum</i>	MZB Cru 4968	1 fov holotype	Indonesia, Lembbeh Strait, LEM.24	Fungiidae: <i>Heliofungia actiniformis</i>
	RMNH.CRUS.D.57575	4fov., 1f., 2m. paratypes	Indonesia, Lembbeh Strait, LEM.28	Fungiidae: <i>Heliofungia actiniformis</i>
	RMNH.CRUS.D.57576	1 fov. paratype	Indonesia, Lembbeh Strait, LEM.28	Fungiidae: <i>Halomitra pileus</i>
	RMNH.CRUS.D.57577	1 fov., 1m. paratypes	Indonesia, Lembbeh Strait, LEM.28	Fungiidae: <i>Heliofungia actiniformis</i>
<i>Per. incertus</i>	RMNH.CRUS.D.53946	1 specimen	Malaysia, Sabah, SEM.48	Porifera: gray encrusting sponge
<i>Pal. pottsi</i>	RMNH.CRUS.D.53933	1 specimen	Malaysia, Sabah, SEM.14	Crinoidea: <i>Comaster spec.</i>

Abbreviations: m., male; f., female; fov, ovigerous female; juv., juvenile.

for Biology, Indonesian Institute of Sciences, Cibinong, Indonesia (MZB).

2.2 Molecular analyses

Total genomic DNA was extracted from eggs or pleopods using the DNeasy Blood & Tissue Kit (QIAGEN, Hilden, Germany). Incubation lasted overnight for approximately 16 hours. The volume in the elution step was decreased to 120 μL to increase the final DNA concentration. For amplifying mitochondrial cytochrome c oxidase I (COI) sequences with a polymerase chain reaction (PCR), the universal primers LCO1490 and HCO2198 (Folmer et al., 1994) were used: 5'-GGTCAACAAAATCATAAAGATATTGG-3' and 5'-TAAACTTCAGGGT-GACCAAAAATCA-3'. The PCR conditions were as follows: 3 min. at 95°C for initial denaturing, followed by 39 cycles of 15 sec. at 95°C, 30 sec. at 49°C, 40 sec. at 72°C with a final extension for 5 min. at 72°C. Each PCR consisted of 2.5 μL CoralLoad PCR buffer (10 \times ; containing 15mM MgCl₂) (QIAGEN), 0.5 μL dNTP's (2.5 mM), 1.0 μL of each primer, 0.3 μL Taq DNA polymerase (5 units/ μL) (QIAGEN). PCR reactions were performed in volumes of 25 μL . Sequences were generated on an Automatic Sequencer 3730xl at Macrogen, Amsterdam. The obtained sequences were edited in Sequencher (vers. 4.10.1) and aligned with the aid of ClustalW Multiple alignment (vers. 1.4, Thompson et al., 1994) incorporated in Bioedit (vers. 5.09, Hall, 2001). Of 602 total aligned sites, 252 were variable and informative for maximum parsimony (MP). Sequences were deposited in GenBank, for which accession numbers were obtained (table 1).

2.3 Data analyses

Palaemonella pottsi (Borradaile, 1915) was selected as outgroup. The best-fitting model for sequence evolution (GTR+G) of the COI dataset was determined by jModelTest (vers. 0.1.1., Posada, 2008), selected by the AIC (Akaike Information Criterion), and was subsequently

applied to the maximum likelihood (ML) analyses with PAUP (vers. 4.0b10, Swofford, 2003) with 100 bootstrap reiterations. A maximum parsimony (MP) tree was constructed using PAUP with 2000 bootstrap reiterations of a simple heuristic search, TBR (tree bisection-reconnection) branch-swapping, and 10 randomly added sequence replications. Transversions were weighted two times over transitions.

2.4 Morphological analyses

In situ underwater photographs of living shrimps on their host were made with a Nikon D5 camera in a Sea & Sea housing. Drawings were made using a Zeiss Discovery V8 and an Olympus BX53 stereo microscope, both with a drawing tube. Drawings were mounted using Adobe Photoshop CS6 software.

2.5 Host coral morphology and phylogeny

In order to clarify the ecological and evolutionary relation between the *Periclimenes* species and their host corals, their association records are projected on a cladogram of the Fungiidae based on published phylogenetic analyses (Gittenberger et al., 2011; Benzoni et al., 2012). In addition, the morphological traits attached vs. free-living mode of life and maximum recorded corallum size are projected on a similar mushroom coral cladogram based on published data (Hoeksema, 1991, 2012, 2014; Gittenberger et al., 2011).

3 Results

3.1 Molecular analyses

Both maximum likelihood and maximum parsimony analyses of COI sequences revealed three well supported clades representing the species *P. diversipes*, *P. watamuae* and an undescribed *Periclimenes* species (fig. 1). Haplotypes of *P. diversipes* specimens are within a range of 0.034 genetic divergence

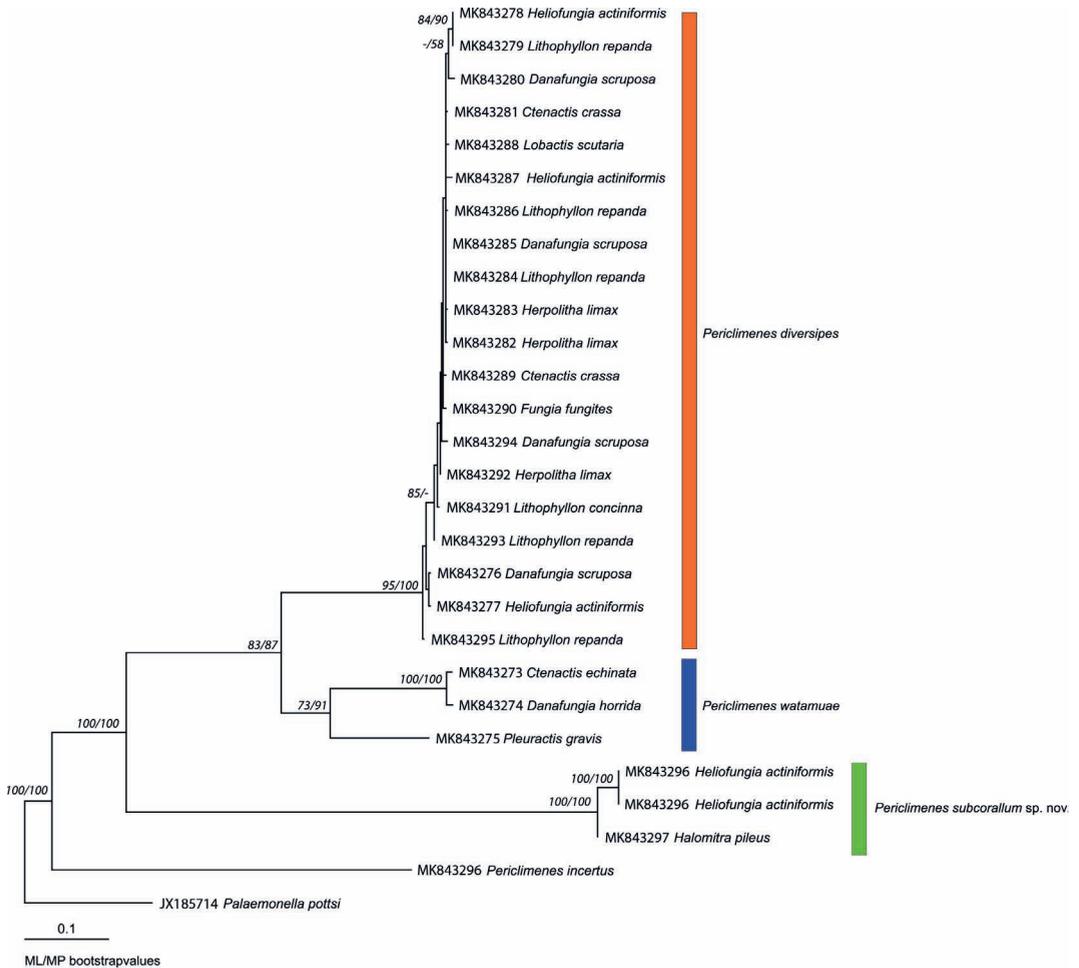


FIGURE 1 Maximum-likelihood tree using the GTR+G substitution model based on COI sequence data of shrimp on mushroom coral species; GenBank accession numbers and host species indicated at end of branches; bootstrap values <50% are not shown; bootstrap values are shown in the order ML/MP.

(table 2). There is no genetic structuring with regards to the different hosts in *P. diversipes*. The genetic distance between *P. watamuae* specimens from *Ctenactis echinata* and *Danafungia horrida* is 0.013. Between these two and the one from *Pleuractis gravis* is 0.187. Morphological differences between specimens from these three hosts were not found. The genetic distance between *Periclimenes subcorallum* sp. nov. specimens on *Heliofungia actiniformis* and *Halomitra pileus* is 0.022.

Periclimenes diversipes was found associated with eight different species of mushroom coral, *P. watamuae* on three, and the new species on two species of mushroom coral (table 3).

3.2 Morphological analyses

Distinguishing morphological features between *P. diversipes* and *P. watamuae* were determined on the basis of specimens used in the molecular analyses: 1) the carpus of the

TABLE 2 JC model (Jukes & Cantor, 1969) divergence matrix for the mitochondrial COI gene of the *Periclimenes* species.

Species	GenBank #	1	2	3	4	5	6	7	8	9	10	11	
1	<i>Per.</i>	MK843273	-										
2	<i>watamuae</i>	MK843274	0.013	-									
3		MK843275	0.187	0.187	-								
4	<i>Per.</i>	MK843276	0.227	0.230	0.223	-							
5	<i>diversipes</i>	MK843277	0.233	0.236	0.229	0.003	-						
6		MK843278	0.253	0.252	0.231	0.029	0.031	-					
7		MK843279	0.251	0.250	0.229	0.026	0.028	0.000	-				
8		MK843280	0.251	0.252	0.238	0.034	0.036	0.012	0.010	-			
9		MK843281	0.254	0.255	0.236	0.026	0.028	0.010	0.007	0.008	-		
10		MK843282	0.256	0.256	0.233	0.025	0.027	0.010	0.007	0.012	0.003	-	
11		MK843283	0.251	0.252	0.233	0.025	0.027	0.010	0.007	0.012	0.003	0.003	-
12		MK843284	0.253	0.254	0.236	0.024	0.026	0.008	0.005	0.010	0.002	0.002	0.002
13		MK843285	0.253	0.254	0.236	0.024	0.026	0.008	0.005	0.010	0.002	0.002	0.002
14		MK843286	0.254	0.255	0.237	0.024	0.028	0.010	0.007	0.012	0.003	0.003	0.003
15		MK843287	0.255	0.256	0.231	0.032	0.033	0.016	0.013	0.018	0.009	0.009	0.009
16		MK843288	0.256	0.256	0.233	0.020	0.026	0.012	0.008	0.012	0.005	0.005	0.005
17		MK843289	0.250	0.251	0.232	0.022	0.026	0.015	0.012	0.017	0.008	0.008	0.008
18		MK843290	0.247	0.250	0.228	0.017	0.022	0.012	0.008	0.017	0.008	0.008	0.008
19		MK843291	0.246	0.247	0.231	0.017	0.020	0.017	0.013	0.019	0.013	0.013	0.013
20		MK843292	0.244	0.245	0.229	0.020	0.021	0.015	0.012	0.013	0.008	0.008	0.008
21		MK843293	0.244	0.246	0.223	0.012	0.014	0.014	0.010	0.019	0.010	0.010	0.010
22		MK843294	0.244	0.245	0.229	0.015	0.019	0.020	0.017	0.019	0.013	0.013	0.013
23		MK843295	0.230	0.232	0.224	0.008	0.008	0.027	0.024	0.029	0.024	0.024	0.024
24	<i>Per.</i>	MK843296	0.369	0.371	0.353	0.343	0.337	0.355	0.353	0.358	0.353	0.352	0.352
	<i>incertus</i>												
25	<i>Per.</i>	MK843296	0.415	0.407	0.390	0.347	0.349	0.363	0.358	0.362	0.358	0.352	0.354
26	<i>subcorallum</i>	MK843296	0.415	0.407	0.390	0.347	0.349	0.363	0.358	0.362	0.358	0.352	0.354
27		MK843297	0.397	0.393	0.379	0.342	0.344	0.360	0.356	0.360	0.355	0.349	0.352
28	<i>Pal. pottsi</i>	JX185714	0.230	0.310	0.290	0.296	0.298	0.323	0.321	0.323	0.321	0.318	0.318

12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
-																
0.000	-															
0.002	0.002	-														
0.007	0.007	0.009	-													
0.003	0.003	0.005	0.011	-												
0.007	0.007	0.005	0.014	0.010	-											
0.007	0.007	0.008	0.014	0.007	0.007	-										
0.012	0.012	0.010	0.019	0.013	0.008	0.008	-									
0.007	0.007	0.008	0.014	0.008	0.007	0.007	0.005	-								
0.008	0.008	0.010	0.016	0.007	0.008	0.003	0.005	0.007	-							
0.012	0.012	0.014	0.019	0.007	0.012	0.008	0.013	0.008	0.008	-						
0.022	0.022	0.024	0.029	0.020	0.022	0.019	0.017	0.014	0.014	0.015	-					
0.350	0.350	0.346	0.351	0.350	0.344	0.352	0.347	0.348	0.346	0.348	0.340	-				
0.354	0.354	0.356	0.370	0.350	0.353	0.348	0.354	0.352	0.343	0.350	0.348	0.402	-			
0.354	0.354	0.356	0.370	0.350	0.353	0.348	0.354	0.352	0.343	0.349	0.348	0.402	0.000	-		
0.352	0.352	0.353	0.364	0.347	0.3478	0.343	0.349	0.347	0.340	0.344	0.345	0.402	0.022	0.022	-	
0.320	0.320	0.314	0.321	0.313	0.317	0.318	0.313	0.316	0.310	0.308	0.305	0.314	0.323	0.323	0.313	-

TABLE 3 Previous (p) and new (n) records of mushroom corals (Fungiidae) acting as host for *Periclimenes* shrimps according to Hoeksema et al. (2012) and the present results.

	<i>P. diversipes</i>	<i>P. goniopora</i>	<i>P. jugalis</i>	<i>P. watamuae</i>	<i>P. subcorallum</i> sp. nov.
<i>Ctenactis crassa</i>	p	-	-	n	-
<i>Ctenactis echinata</i>	-	p	-	n	-
<i>Danafungia horrida</i>	-	-	-	n	-
<i>Danafungia scruposa</i>	n	-	-	n	-
<i>Fungia fungites</i>	n	p	-	-	-
<i>Halomitra pileus</i>	n	-	-	p, n	n
<i>Heliofungia actiniformis</i>	p, n	-	p	p, n	n
<i>Herpolitha limax</i>	n	-	-	p, n	-
<i>Lithophyllon concinna</i>	n	-	-	-	-
<i>Lithophyllon repanda</i>	n	p	-	-	-
<i>Lobactis scutaria</i>	n	-	-	-	-
<i>Pleuraetis gravis</i>	-	-	-	n	-
<i>Polyphyllia talpina</i>	-	-	-	p	-
<i>Sandalolitha robusta</i>	n	p	-	-	-

major second pereopod of *P. diversipes* (fig. 2) is 2–3 times as long as its distal width whereas it is as long as its distal width in *P. watamuae* (fig. 3); 2) the carpus of the minor second pereopod of *P. diversipes* (fig. 4) is 3–4 times as long as its distal width whereas it is 1.5–2 times as long as its distal width in *P. watamuae* (fig. 5).

3.3 Colour

On the basis of molecular analyses, colour differences between *P. diversipes* and *P. watamuae* were determined. *Periclimenes diversipes* has oblong oblique red spots on carapace and abdomen and faint transverse white bands on the abdominal segments (fig. 6) whereas *P. watamuae* has longitudinal red lines over carapace and abdomen, a more distinct transverse white band on the

posterior part of the carapace, dorsolateral white spots on both sides on the second abdominal segment, and a clear transverse white band at the level of the fourth abdominal segment (fig. 7A, B).

3.4 Host range

With the use of the distinguishing features on the second chelipeds, a larger collection of symbiotic shrimps from mushroom corals could be identified (table 1). Based on earlier records and the present results, *P. diversipes* was found associated with nine mushroom coral species, all of which except one represent new host records (table 3): *Danafungia scruposa* (Klunzinger, 1879), *Fungia fungites*, *Halomitra pileus*, *Heliofungia actiniformis*, *Herpolitha limax*, *Lithophyllon concinna* (Verrill, 1864), *L. repanda*, *Lobactis scutaria*

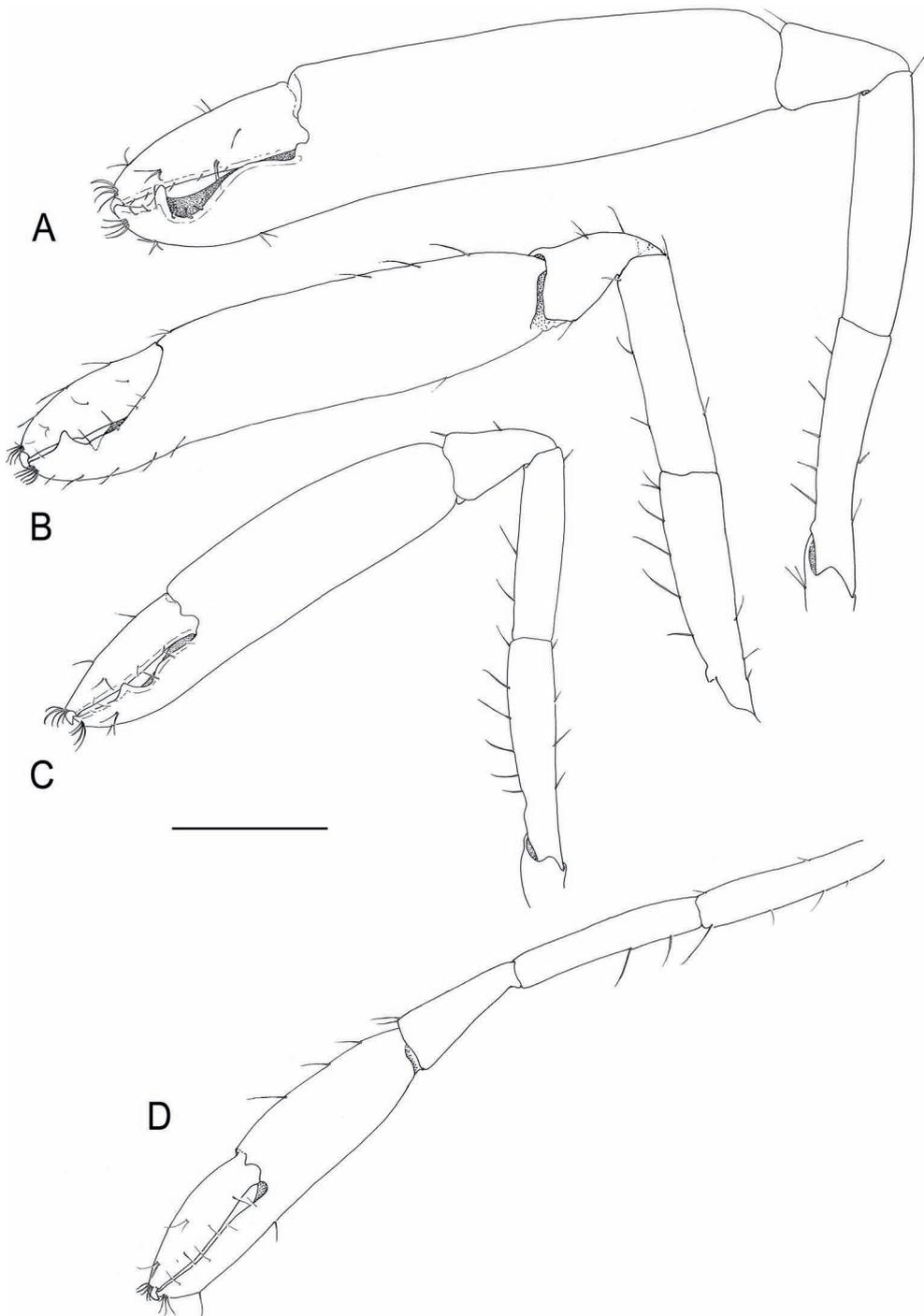


FIGURE 2 *Periclimenes diversipes* Kemp, 1922, major second pereopod. A, ovigerous female pochl. 1.63 mm, left P2, RMNH.CRUS.D.57551, GenBank MK843282; B, ovigerous female pochl. 1.25 mm, right P2, RMNH.CRUS.D.57547, GenBank MK843284; C, female pochl. 1.25 mm, left P2, RMNH.CRUS.D.57548, GenBank MK843295; D, male, pochl. 1.38 mm, right P2, RMNH.CRUS.57553, GenBank MK843283. Scale bar = 0.4 mm.

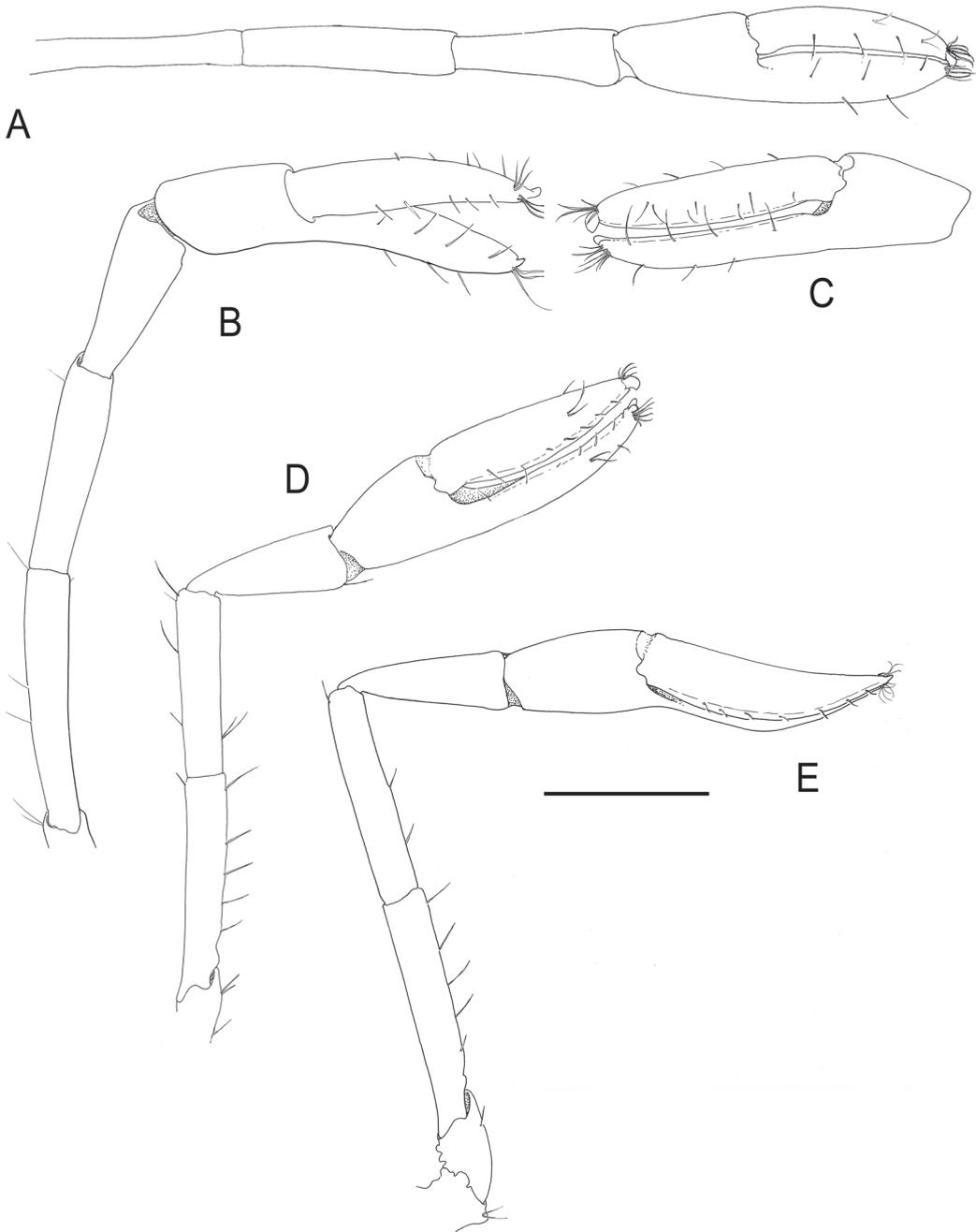


FIGURE 3 *Periclimenes diversipes* Kemp, 1922, minor second pereiopod. A, male, pocl 1.38 mm, left P2, RMNH.CRUS.D.57553, GenBank MK843283; B, ovigerous female pocl. 1.25 mm, left P2, RMNH. CRUS.D.57547, GenBank MK843284; C, idem, lateral aspect chela; D, female pocl. 1.25 mm, right P2, RMNH.CRUS.D.57548, GenBank MK843295; E, ovigerous female pocl. 1.63 mm, right P2, RMNH. CRUS.D.57551, GenBank MK843282. Scale bar = 0.4 mm.

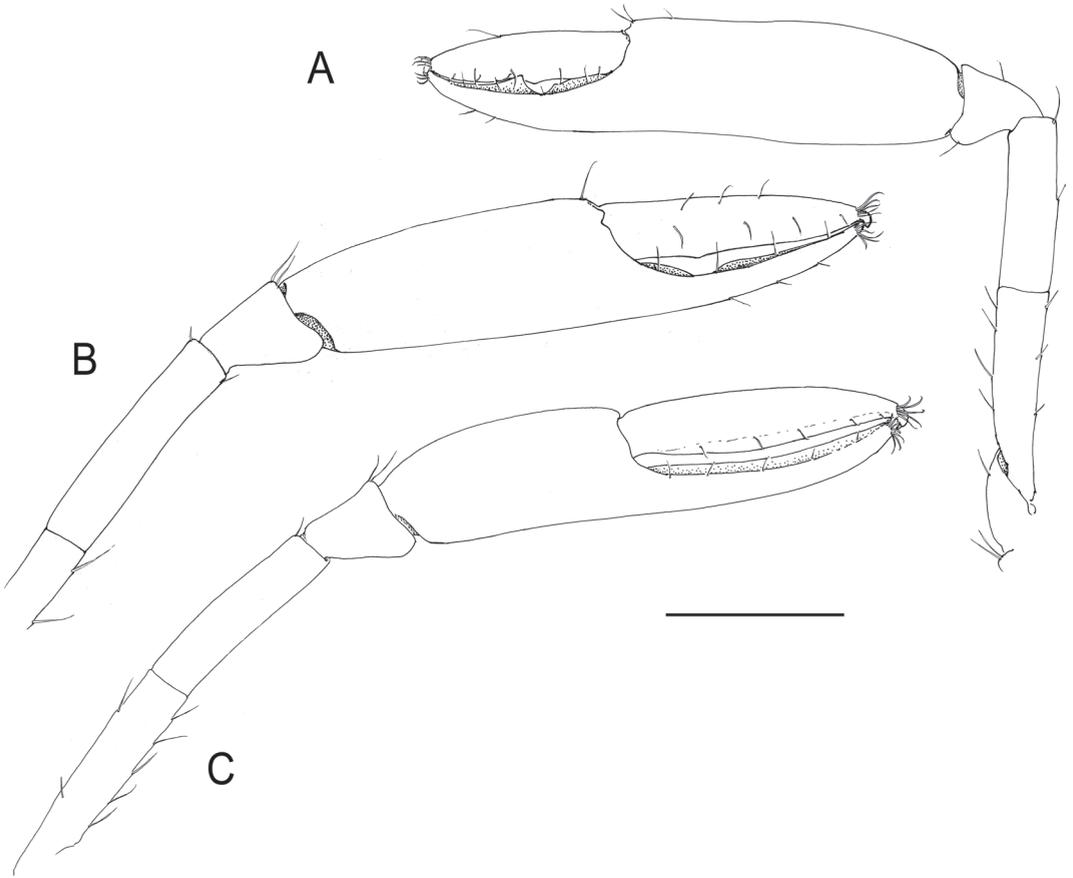


FIGURE 4 *Periclimenes watamuae* Bruce, 1976a, major second pereiopod. A, male, pocl 1.00 mm, right P2, RMNH. CRUS.D.57574, LEM.36; B, ovigerous female, pocl 1.45 mm, left P2, RMNH. CRUS.D.57574, LEM.36; C, ovigerous female, pocl. 1.40 mm, left P2, RMNH. CRUS.D.57574, GenBank MK843275. Scale bar = 0.4 mm.

(Lamarck, 1801), and *Sandalolitha robusta*. *Periclimenes watamuae* was found associated with seven mushroom coral species of which five constitute new host records (table 3): *Ctenactis crassa*, *C. echinata*, *Danafungia horrida* (Dana, 1846), *D. scruposa*, *Heliofungia actiniformis*, *Herpolitha limax*, and *Pleuractis gravis* (Nemenzo, 1955). The new *Periclimenes* species was found on *Halomitra pileus* and *Heliofungia actiniformis* (table 3).

The closely related *P. diversipes* and *P. watamuae* are both associated with a wide range of mushroom corals, consisting of ten and nine species, respectively (table 3).

They have three mushroom coral species in common that act as hosts. However, no genetic structuring within this shrimp species with regards to host choice could be detected.

The mushroom coral cladogram (fig. 8) shows that none of the *Periclimenes* species has ever been recorded from an attached mushroom coral species (A = attached) and from species with a maximum recorded size < 15 cm (S = small). Coral species of the genus *Cycloseris* fit in these categories and are therefore not recorded as hosts. The host species can be found among free-living, coral species with a maximum

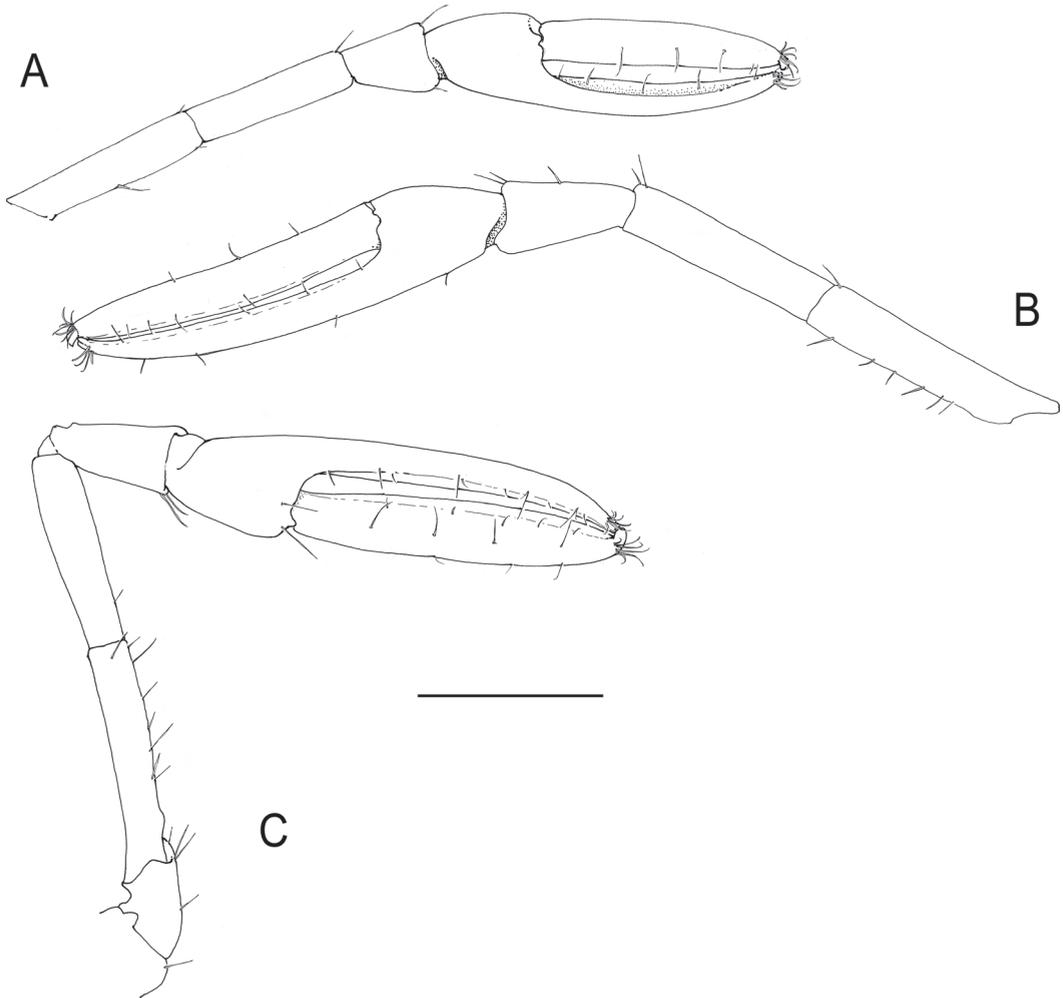


FIGURE 5 *Periclimenes watamuae* Bruce, 1976a, minor second pereiopod. A, male, 1.00 mm, left P2, RMNH.CRUS.D.57574, LEM.36; B, ovigerous female, pocl. 1.45 mm, right P2, RMNH.CRUS.D.57574, LEM.36; C, ovigerous female, pocl. 1.40 mm, right P2, RMNH.CRUS.D.57574, GenBank MK843275. Scale bar = 0.4 mm.

diameter > 15 cm, which together do not form a monophyletic group within the Fungiidae (fig. 8).

3.5 Systematic account

Family Palaemonidae Rafinesque, 1815

Genus *Periclimenes* O.G. Costa, 1844

Periclimenes subcorallum Fransen & Rauch, sp. nov.

(Figs. 9–13)

<http://zoobank.org/urn:lsid:zoobank.org:act:5129C847-F357-4363-B5A8-96869C3FD144>

Material examined. Indonesia, NE Sulawesi, Lembeh Strait. Ovigerous female holotype (pocl. 1.50mm) MZB Cru 4968; 4 ovigerous female paratypes (pocl. 1.45–1.78 mm, 1 non-ovigerous female (pocl. 1.38 mm), 2 males (pocl. 1.35 and 1.40 mm) RMNH.CRUS.D.57575: stn LEM.24, Tanjung Pandea, 1°23' 52"N 125°09'58"E, 11.ii.2012, depth

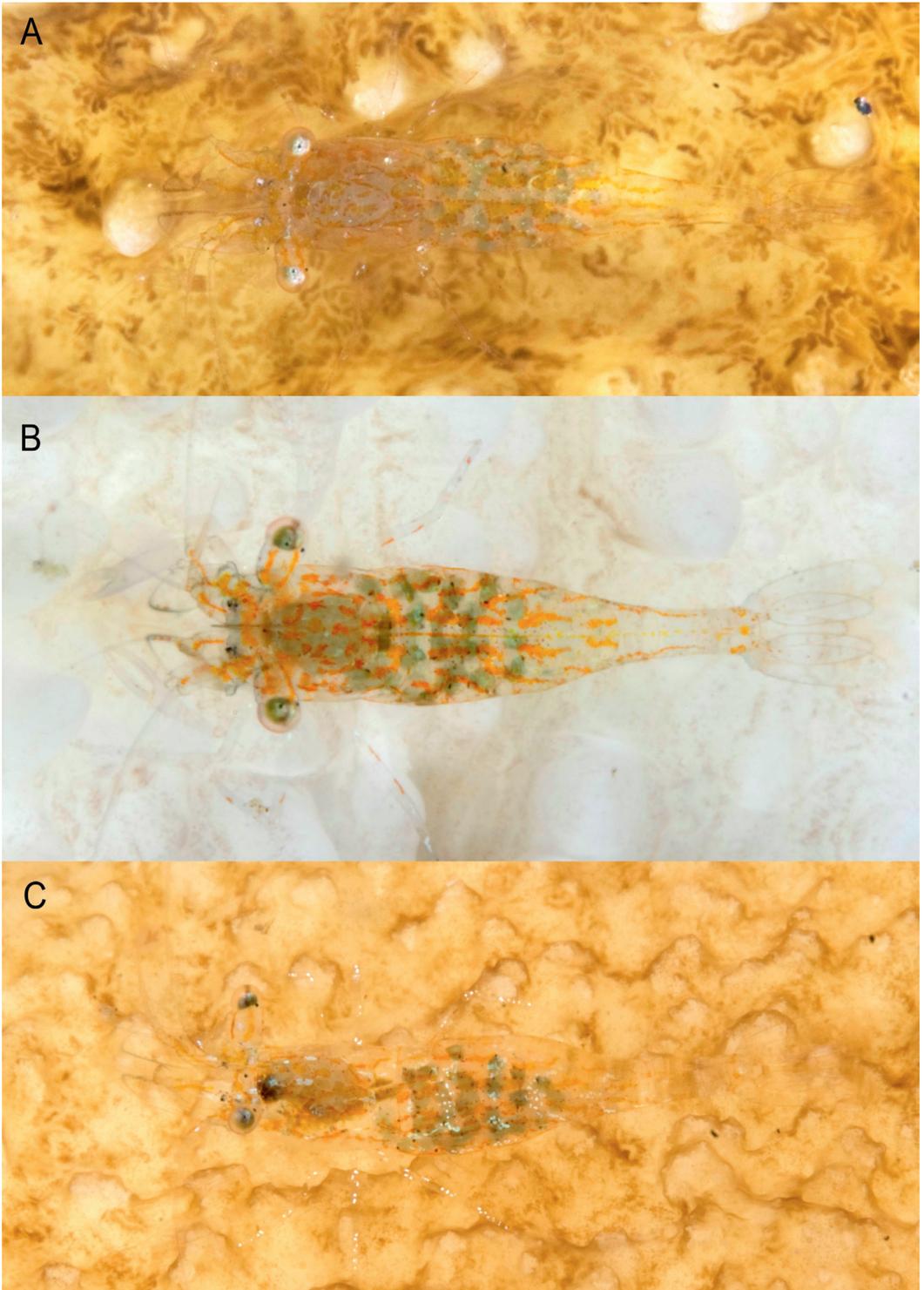


FIGURE 6 *Periclimenes diversipes* Kemp, 1922, ovigerous female. A, stn LEM.07, on *Danafungia scruposa*; B, stn LEM.07, on *Lithophyllon repanda*; C, stn LEM.18, on *Sandalolitha robusta*.

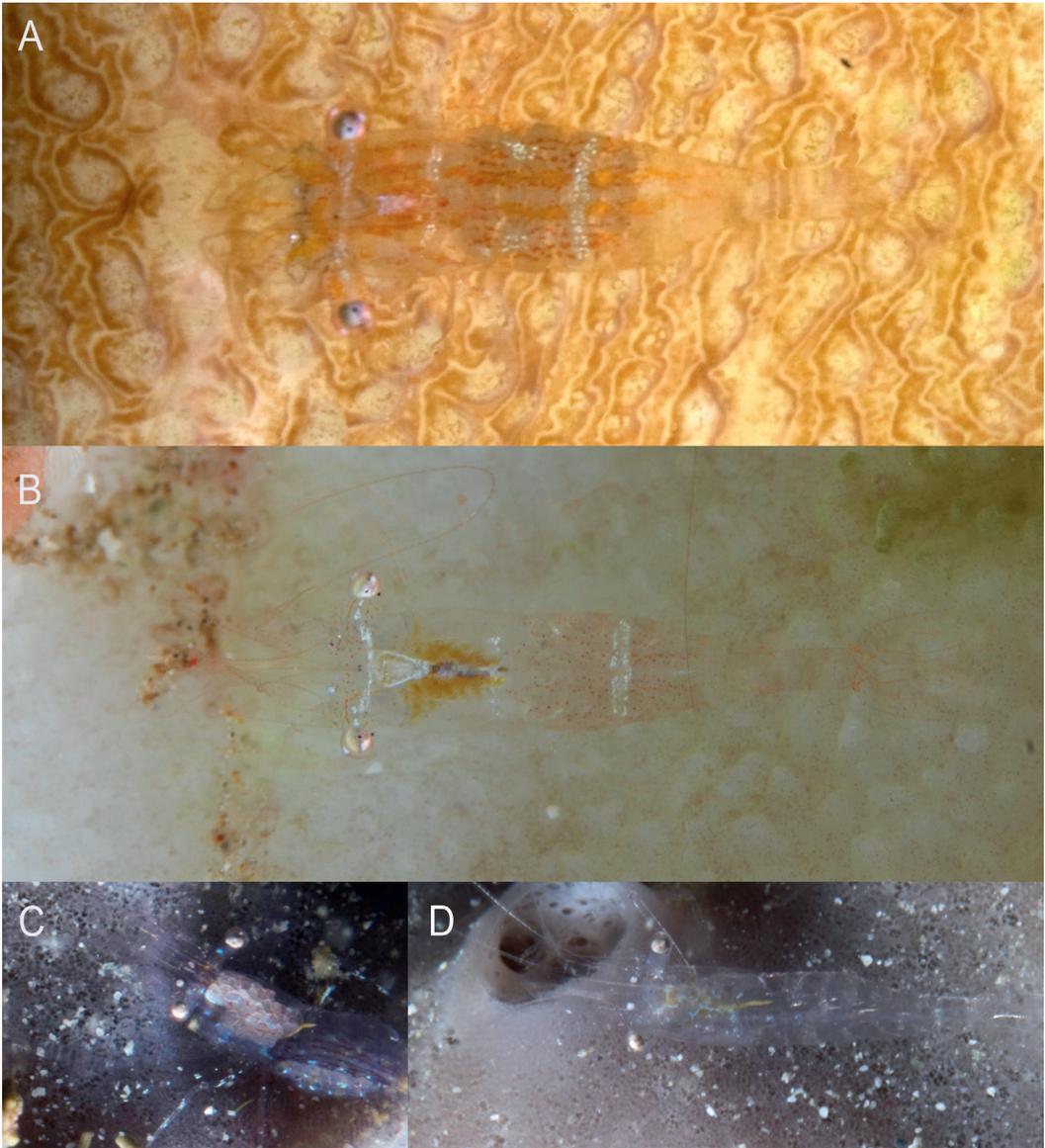


FIGURE 7 A–B, *Periclimenes watamuae* Bruce, 1976a, ovigerous female; C–D, *Periclimenes incertus* Borradaile, 1915. A, stn LEM.26, on *Lobactis scutaria*; B, stn TER.16, on *Polyphyllia talpina*; C–D, stn SEM.48, on sponge; C, ovigerous female; D, male.

7 m, on *Heliofungia actiniformis*, coll. Cessa Rauch. — 1 ovigerous female (pocl. 1.25 mm) and 1 male (pocl. 1.18 mm) paratypes, RMNH. CRUS.D.57577: stn LEM.28, Desa Pandean, 1°24'21"N 125°10'52"E, 14.ii.2012, depth 13.2 m, on *Heliofungia actiniformis*, coll. Cessa Rauch. — 1 ovigerous female (pocl. 1.63 mm) paratype,

RMNH.CRUS.D.57576: stn LEM.28, Desa Pandean, 1°24'21"N 125°10'52"E, 14.ii.2012, depth 20 m, on *Halomitra pileus*, coll. C.H.J.M. Franssen.

Comparative material examined. *Periclimenes incertus* Borradaile, 1915 (figs. 8C, D, 14–16). **Malaysia, Sabah, Semporna.** 27 ovigerous females, 2 non-ovigerous females, 15 males

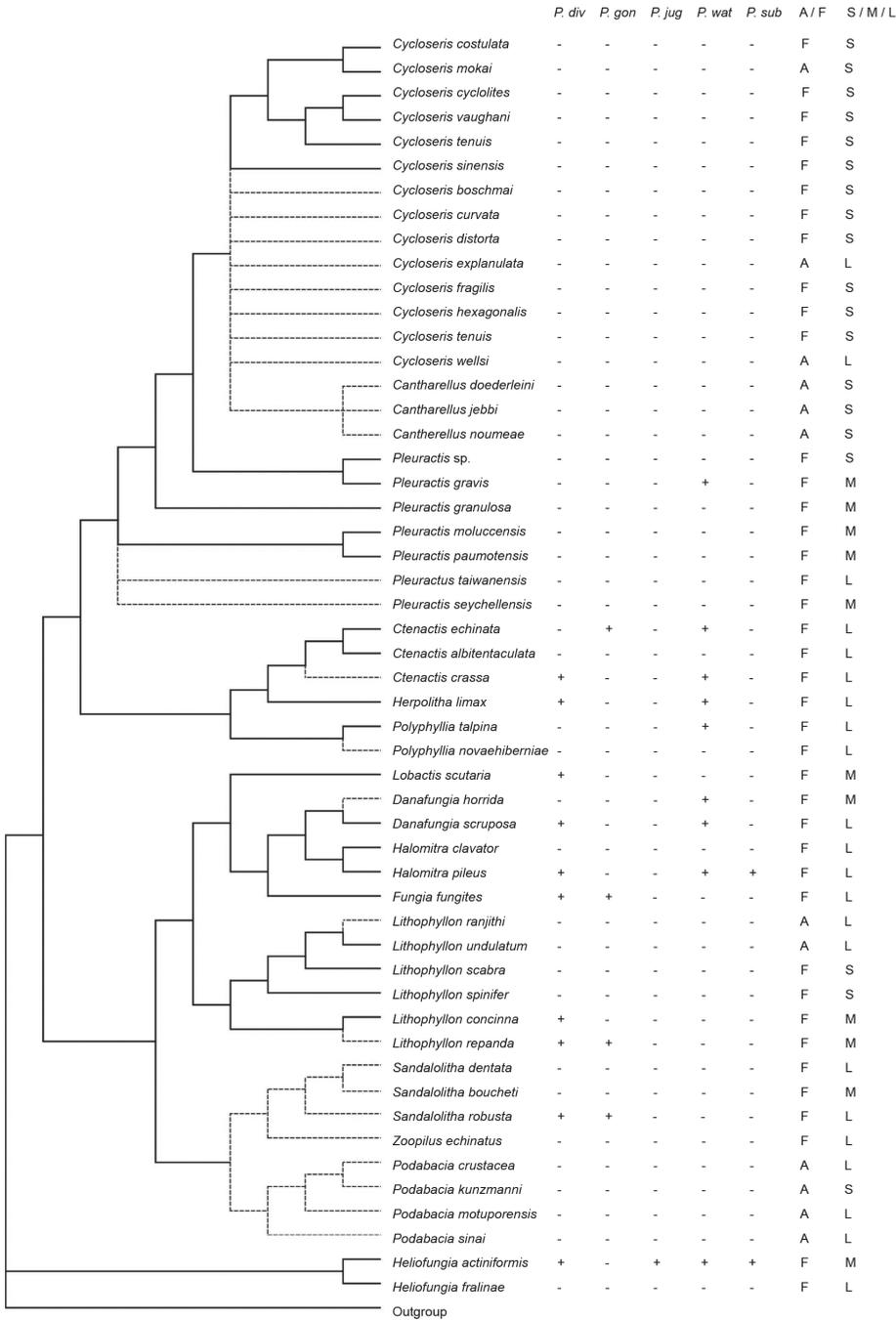


FIGURE 8 Mushroom coral cladogram based on published phylogenetic analyses (Gittenberger et al., 2011; Benzoni et al., 2012). The host relations of five *Periclimes* species (table 3) are projected on the phylogeny reconstruction as well as the morphological traits “attached vs. free-living mode of life” (A = attached / F = free-living) and maximum recorded corallum size (Hoeksema, 1991, 2012a, 2014; Gittenberger et al., 2011) with size categories (S = small, < 15 cm; M = medium, ≥15 cm and < 25 cm; L = large, ≥25 cm). *P. div* = *Periclimes diversipes*, *P. gon* = *Periclimes goniopora*, *P. jug* = *Periclimes jugalis*, *P. wat* = *Periclimes watamuae*, *P. sub* = *Periclimes subcorallum* sp. nov.

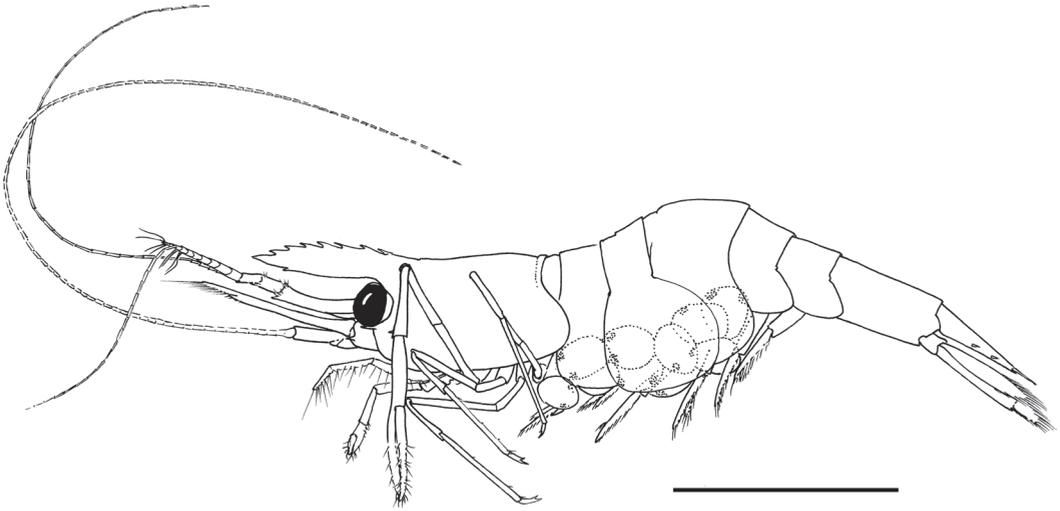


FIGURE 9 *Periclimenes subcorallum* sp. nov., ovigerous female holotype (pocl. 1.50 mm), MZB CRU 4968. Habitus. Scale = 2 mm.

and 6 juveniles (pocl. 1.00–2.08 mm), RMNH. CRUS.D.53946: stn SEM.48, Timbun Mata Isl., 04°37'59.6"N 118°35'21.6"E, 15.xii.2010, depth 22 m, on grey encrusting sponge, coll. C.H.J.M. Fransen.

Description. Small-sized, rather slender palaemonid shrimp, with slender pereopods (fig. 9).

Carapace smooth. Rostrum (fig. 10A, B) well developed, reaching halfway distal segment of antennular peduncle; lamina deep, lateral carina indistinct, situated near to proximally slightly convex ventral margin with 1 sub-distal tooth; convex posterior part of ventral margin with double row of plumose setae; dorsal margin convex, elevated, strongly compressed, with 6 subequal teeth, posteriormost situated at level of posterior margin of orbit; 2–3 plumose setae just in front of each dorsal teeth. Supra-orbital spines absent. Inferior orbital angle well developed, produced, angular in lateral view. Antennal spine of moderate size, marginal, situated below inferior orbital angle. Hepatic spine about as large as antennal spine, situated well behind level of posterior orbital margin and slightly below level of

antennal spine. Antero-lateral angle of carapace blunt, not produced.

Abdominal segments (fig. 9) smooth. Third segment not produced posterodorsally. Pleura all broadly rounded. Sixth abdominal segment 2.3 times as long as fifth (relatively longer in smaller specimens), posteroventral angle feebly produced, rounded, posterolateral angle acute.

Telson (fig. 14A) 0.1 times as long as sixth abdominal segment and 3.0 times longer than anterior width; lateral margins converge posteriorly; two pairs of submarginal dorsal spines present at 0.59 and 0.82 of telson length, posterior margin (fig. 14B) rounded, 0.36 of anterior width, with three pairs of spines. Lateral spines short, as long as dorsal spines. Intermediate spines well developed, about 0.22 of telson length, 2.2 times length of submedian spines.

Eyes (fig. 10A, B) well developed. Cornea globular, with distinct accessory pigment spot posterodorsally. Eyestalks almost twice as long as proximal width, slightly swollen proximally.

Antennular peduncle (fig. 10A, B) exceeding tip of rostrum by half of distal segment.

Proximal segment long, slender, 2.5 times longer than wide; stylocerite slender, acute, reaching almost to middle of segment; lateral margin straight, anterolateral margin produced, rounded, with distolateral tooth and row of setae; ventral margin with small submedian tooth at about 0.4 of length of segment. Statocyst containing granular statolith. Intermediate and distal segments short, together equal to 0.48 of proximal segment length. Upper flagellum biramous, with the first 5–7 segments fused; short ramus with 3 segments; aesthetascs present on short free ramus only. Longer free ramus long and slender, with about 25 segments. Lower flagellum very long and slender, almost twice as long as longer free ramus of upper flagellum.

Antennal basicerite (fig. 10B) with strong lateral tooth. Ischiocerite and merocerite normal. Carpocerite slender, reaching 0.4 of length of scaphocerite. Scaphocerite long, rather slender, with lamella distinctly overreaching distal margin of antennular peduncle. Lateral border straight, ending in acute large distolateral tooth. Lamella extending beyond distolateral tooth, feebly angulated distomedially, about 3.5 times longer than broad, with greatest width at about one half of its length.

Epistome, labrum and paragnath without special features.

Second thoracic sternite (fig. 10G) formed into broad triangular medially rounded process between second maxillipeds.

Third thoracic sternite unarmed (fig. 10G).

Fourth thoracic sternite with broad medial triangular plate with median notch posteromedial of first pereopods (fig. 10G).

Fifth thoracic sternite with shallow lateral plates posteromedial of second pereopods.

Sixth to eighth thoracic sternites broad, unarmed.

Mandible (fig. 10C) with cylindrical molar process with blunt teeth on strong chewing surface, with 2 short bands of few setae subdistally. Incisor process slender, with 3 well

developed teeth distally, of which later almost slightly enlarged. Mandible without palp.

Maxillula (fig. 10D) with upper lacinia rectangular with rows of few serrulate spines and slender setae medially; lower lacinia slender, with few serrulate setae distally; palp bilobed, medial lobe with single short recurved simple seta.

Maxilla (fig. 10E) with short tapering palp with few plumose setae laterally. Basal endite bilobed, distal lobe slightly broader than proximal lobe, both lobes with row of about 10 minutely serrate setae medially. Coxal endite obsolete, median margin convex, without setae. Scaphognathite normal, widest centrally, about 2.9 times longer than broad, with marginal plumose setae.

First maxilliped (fig. 10F) with short, slender, tapering palp without setae. Basal region broad, not distinctly separated from the coxal region, with median margin provided with setulose and slender simple setae. Coxal region strongly convex with few minutely serrulate setae and 2 large long plumose setae medially. Caridean lobe with coarsely setulose plumose marginal setae. Flagellum of exopod well developed with 4 long plumose distal setae. Epipod bilobed.

Second maxilliped (fig. 11A) with dactylar segment narrow, about 3.0 times longer than wide, straight medially, densely fringed with numerous coarsely serrulate, spiniform, and long curled finely serrulate setae medially. Propodal segment longer than dactylar segment twice as long as wide, with distomedial margin not produced, with few long serrulate setae. Carpus short, unarmed. Merual segment short, not excavate, without setae. Ischium completely fused to basis. Basis with long slender exopod about as long as length of endopod, with 4 long plumose setae distally and few shorter plumose seta subdistally. Coxa slightly produced medially, with 2 long setae medially, small oblong epipod laterally.

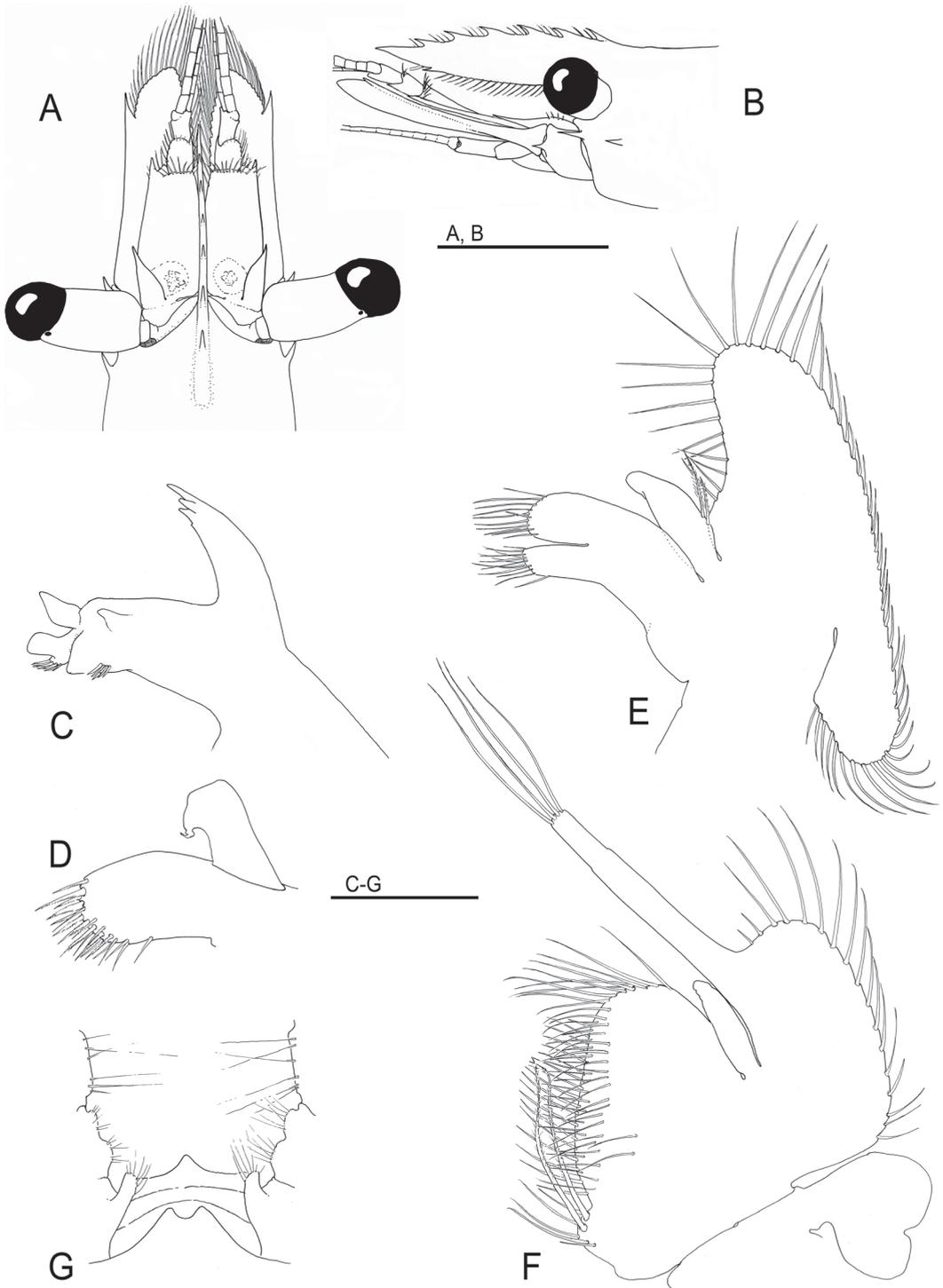


FIGURE 10 *Periclimenes subcorallum* sp. nov., ovigerous female paratype (pocl. 1.45 mm), RMNH.CRUS.D.57575. A, rostrum and anterior appendages, dorsal view; B, idem, lateral view; C, left mandible; D, left maxillula; E, left maxilla; F, left first maxilliped; G, fourth thoracic sternites and proximal segments of first pereiopods. Scale bar: A, B = 1 mm; C-F = 0.2 mm; G = 0.4 mm.

Third maxilliped (fig. 11B) slender. Terminal segment 3.5 times longer than proximal width, 0.57 of length of penultimate segment, with rows of short serrulate setae medially and longer simple setae ventrolaterally. Penultimate segment slender, 4.12 times longer than wide with rows of long finely serrulate setae medially and ventrolaterally. Ischiomerus and basis fused, combined segment 1.50 times as long as penultimate segment, 4.78 times as long as distal wide; proximomedial margin rounded with few simple setae followed by row of 5 short serrulate setae, meral part with row of long minutely serrulate setae, with one subdistal lateral spine. Exopod reaching 0.8 of combined segment, with 4 distal and 3 subdistal plumose setae. Coxa not produced medially, with rounded lateral plate, without arthrobranch.

First pereopod (fig. 11C) slender, reaching to end of scaphocerite. Chela (fig. 11E) with palm subcylindrical, straight, 1.6 times longer than wide. Fingers as long as palm, straight not subs spatulate, with brushes of few setae in distal part, cutting edges entire, tips of fingers hooked. Cleaning setae present proximally on palm and distoventral part of carpus. Carpus 1.3 times length of chela, 5.0 times longer than wide. Merus slightly longer than carpus, twice length of ischium. Ischium with medial setal ridge with few long simple setae. Basis with proximomedial setal ridge and distomedial small setose process. Coxa with setose medial process (fig. 11D).

Second pereopods (fig. 12A, D), equal in length, dissimilar. Major left second pereopod (fig. 12A) extending beyond antennular peduncle with chela. Chela with palm subcylindrical, straight, 3.6 times as long as wide. Fingers (fig. 12B) 0.41 of palm length. Dactylus as wide as fixed finger, fingers gaping in middle, both with brushes of setae in distal part, tips (fig. 12C) strongly hooked. Dactylus with cutting edge with one triangular tooth proxi-

mally of gape and one triangular tooth distally of gape, cutting edge of gape rounded, that between distal tooth and hooked tip acute. Fixed finger with three blunt teeth proximally of gape and one triangular tooth distally of gape, cutting edge of gape rounded, that between distal tooth and hooked tip acute. Carpus gradually increasing in width distally, merus and ischium unarmed, their length ratios of 0.37, 0.69 and 0.80 times length of palm. Basis with few setae medially. Coxa with small median setose process. Minor second chela (fig. 12D) with fingers 0.8 times length of subcylindrical palm, with setal brushes, fingers (fig. 12E) distally hooked, cutting edges with small triangular tooth in middle, acute distally of tooth, rounded proximally. Carpus gradually increasing in width distally; merus and ischium unarmed, their length ratios of 0.81, 1.04 and 1.26 times length of palm. Basis and coxa as in major chela.

The ambulatory pereopods (fig. 13A, C, E) slender, similar in form, slightly increasing in length from third to fifth pereopod, reaching with dactyli to distal margin of scaphocerite. Dactylus of third pereopod (fig. 13B) slender, not tapering, 0.24 of propodus length, 4.1 times as long as proximal width, with large accessory tooth reaching to 0.75 of slightly curved unguis length, accessory tooth and unguis with same proximal height; flexor margin of corpus concave with series of 5 small denticles. Propodus 12 times longer than wide, with two distoventral spines and 2 small ventral spines; distoventral spines with fine denticulation on flexor margin. Carpus, merus and ischium 0.50, 1.10 and 0.50 of propodus length, unarmed. Fourth (fig. 13C, D) and fifth (fig. 13E, F) pereopods similar as third, fourth with 3 ventral teeth, fifth with 1 ventral tooth on propodus.

Endopod of first pleopod in ovigerous female short (fig. 14D), 0.4 of length of exopod, with long plumose setae along its entire

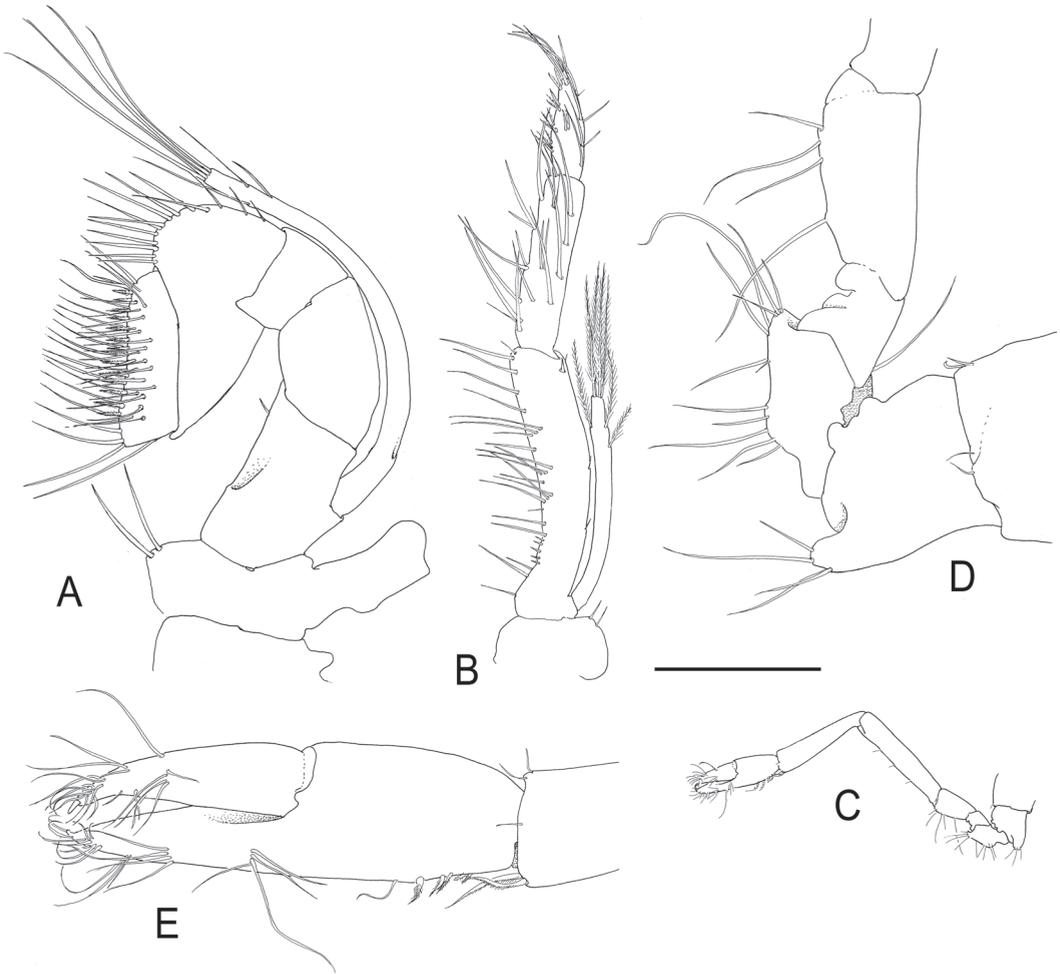


FIGURE 11 *Periclimenes subcorallum* sp. nov., ovigerous female paratype (pocl. 1.45 mm), RMNH.CRUS.D.57575. A, left second maxilliped; B, left third maxilliped; C, left first pereiopod; D, idem, proximal segments; E, idem, chela. Scale bar: A, D, E = 0.2 mm; B = 0.4 mm; C = 1 mm.

margin. Endopod of first pleopod in male (fig. 14E) short, 0.4 times length of exopod, distally broadly rounded with median lobe, with few long plumose setae along lateral margin and about 6 very short simple setae in proximal 2/3rd of medial margin. Endopod of second pleopod in male (fig. 14F) slightly shorter length of exopod. Appendix masculina long and slender, almost twice as long as

appendix interna, with five serrate long setae distally.

Uropods extending beyond tip of telson. Protopodite unarmed laterally. Exopod with lateral border almost straight, slightly setose in proximal part, terminating in a small distolateral tooth with mobile spine medially, mobile spine twice as long as distolateral tooth (fig. 14C).

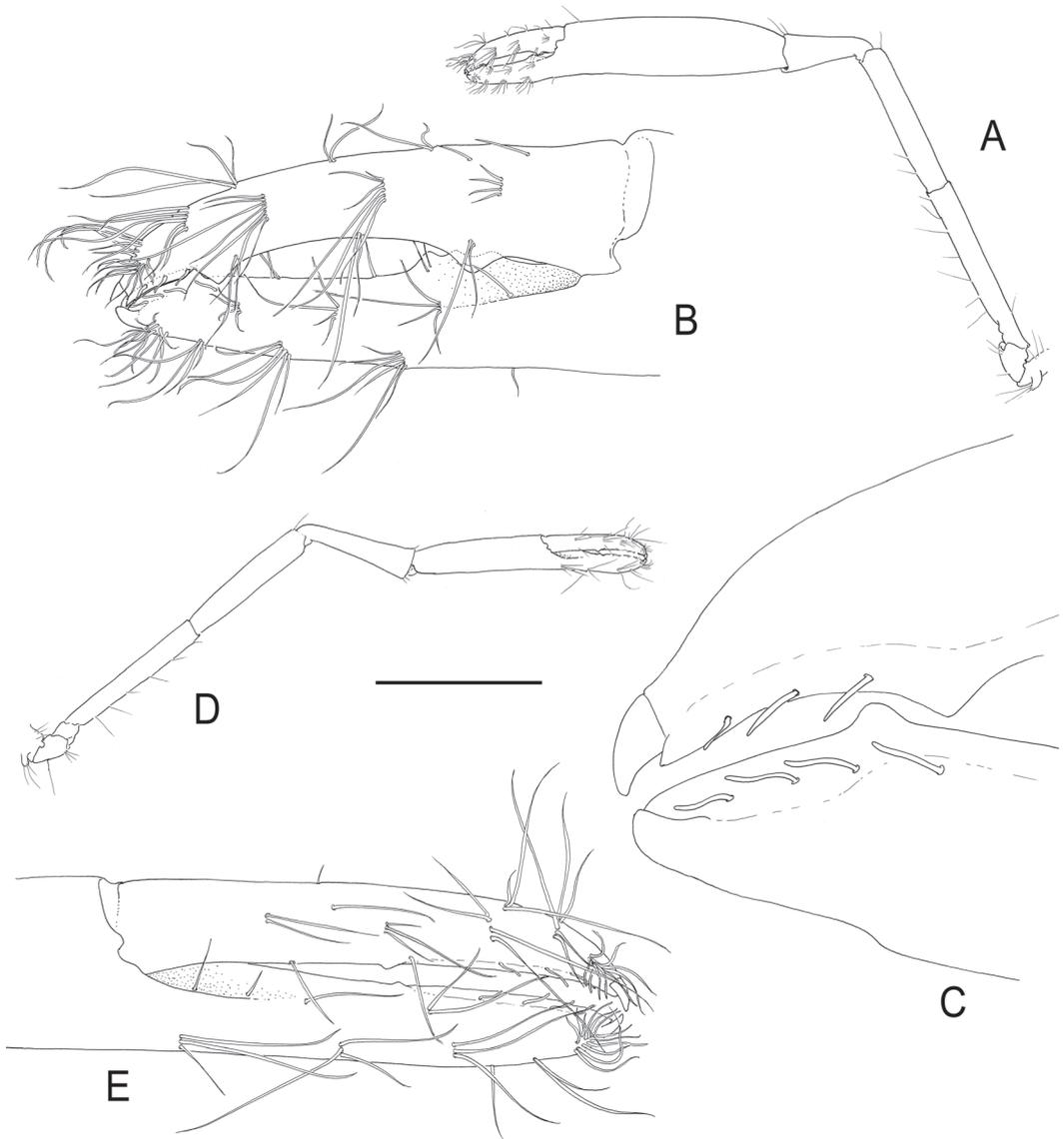


FIGURE 12 *Periclimenes subcorallum* sp. nov., ovigerous female paratype (pocl. 1.45 mm), RMNH.CRUS.D.57575. A, left major second pereiopod; B, idem fingers of chela; C, idem, tip of fingers, setae omitted; D, right minor second pereiopod; E, idem, fingers of chela. Scale bar: A, D = 1 mm; B, E = 0.2 mm; C = 0.07 mm.

About 25 eggs of ca. 0.4mm in diameter present under abdomen.

Colouration. Not known.

Etymology. The epithet 'subcorallum' refers to the observed position of the shrimps in relation their hosts, underneath corals.

Host records. *Heliofungia actiniformis* and *Halomitra pileus* (Fungiidae, Scleractinia).

Systematic position. The new species belongs to the *Periclimenes obscurus* species group comprising: *P. batei* (Borradaile, 1917); *P. burrup* Bruce, 2007; *P. delagoae* Barnard,

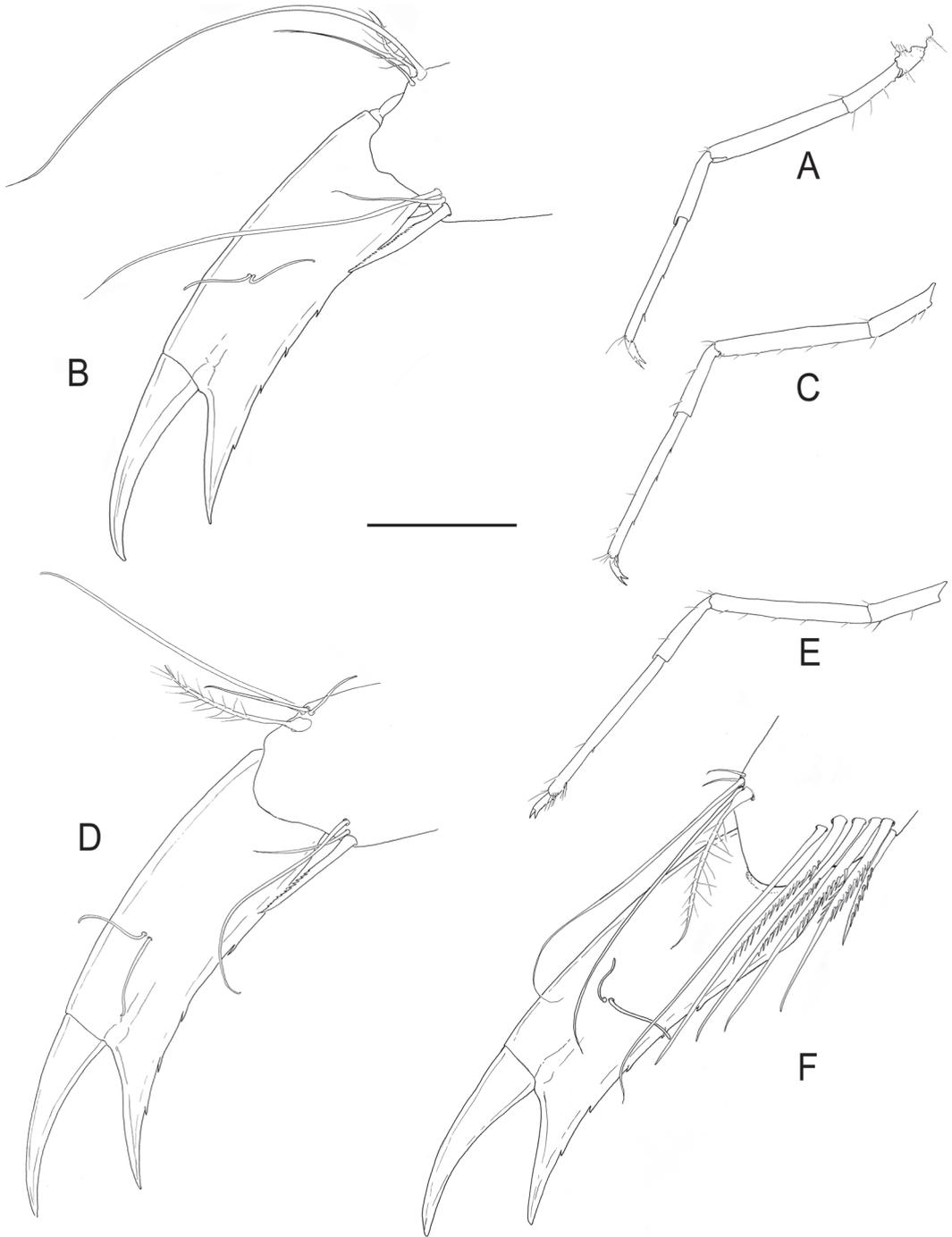


FIGURE 13 *Periclimenes subcorallum* sp. nov., ovigerous female paratype (pocl. 1.45 mm), RMNH.CRUS.D.57575. A, left third pereopod; B, idem, dactylus; C, left fourth pereopod; D, idem, dactylus; E, left fifth pereopod; F, idem, dactylus. Scale bar: A, C, E = 1 mm; B, D, F = 0.07 mm.

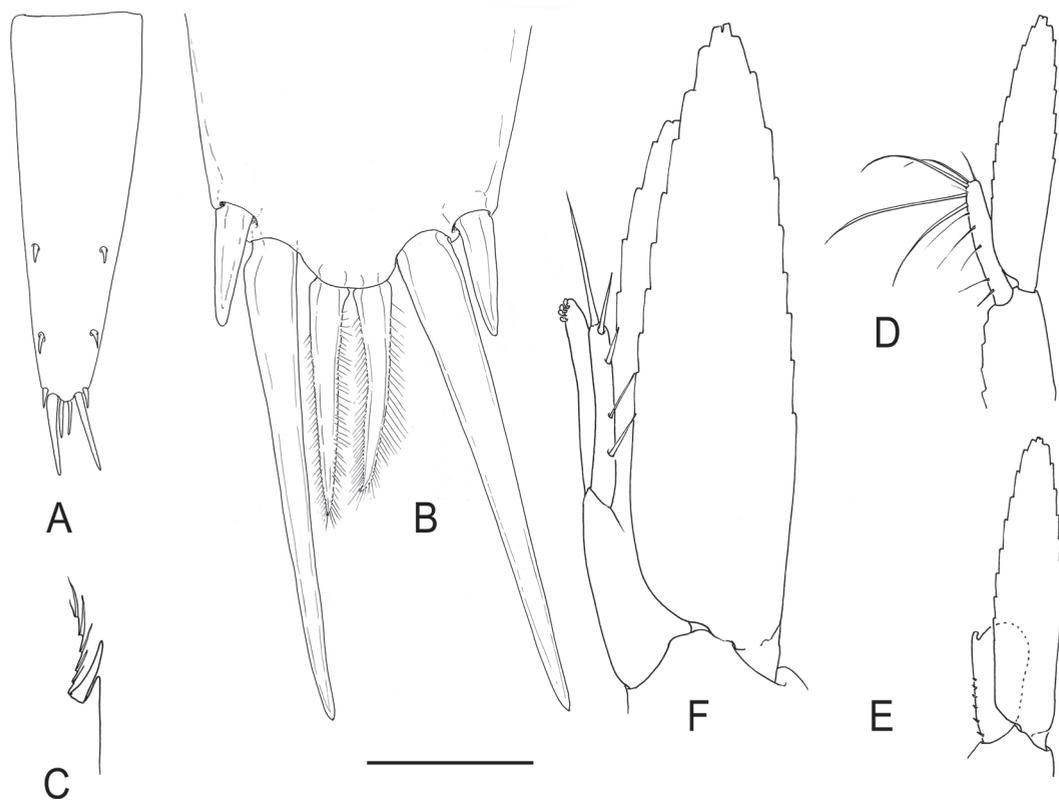


FIGURE 14 *Periclimenes subcorallum* sp. nov., ovigerous female paratype (pocl. 1.45 mm), RMNH.CRUS.D.57575. A, telson; B, idem, detail distal part; C, distolateral part of uropod exopod; D, right first pleiopod. Male paratype (pocl. 1.35 mm), RMNH.CRUS.D.57575. E, right first pleiopod; F, right second pleiopod. Scale bar: A, C, E = 0.4 mm; B = 0.07 mm; D, F = 0.2 mm.

1958; *P. hongkongensis* Bruce, 1969; *P. incertus* Borradaile, 1915; *P. macrorhynchia* Eilbracht & Fransén, 2015; *P. nomadophila* Berggren, 1994; *P. obscurus* Kemp, 1922; *P. sinensis* Bruce, 1969; *P. terangeri* Bruce, 1998; *P. toloensis* Bruce, 1969; *P. zeviniae* Đuriš, 1990 (Bruce, 1969, 1987, 2007; Đuriš, 1990; Berggren, 1994; Eilbracht & Fransén, 2015). Species in the group have a well-developed, horizontal rostrum with a moderately deep lamina bearing numerous dorsal teeth and 0 to 2 ventral teeth; the antennal spine is well developed, a supraorbital spine is absent, the epigastric spine is present or absent; the inferior orbital angle is feebly produced; the fourth thoracic sternite is without a slender median process; the third

abdominal segment is not conspicuously produced posterodorsally; the first pereopods have simple or 'nail-like' fingers and a more or less developed setose distoventral process on the coxa; the second pereopods are slender, unspecialized, carpus more than one third of length of palm, merus unarmed; dactylus of ambulatory pereopods usually biunguiculate. The delimitation of the group is rather vague and seems to overlap with species from the *P. diversipes* and *P. granulimanus* species groups.

The new species is most similar to *P. incertus* Borradaile, 1915 and *P. zeviniae* Đuriš, 1990. Both species share the denticulate ventral margin of the corpus of the ambulatory

pereiopods with the new species. These three species also have the accessory tooth of the dactyli of the ambulatory pereiopods as stout as or stouter than the unguis, and almost as long as the unguis, whereas most other species in the *P. obscurus* species group have the accessory tooth less stout than the unguis and half the length of the unguis or less, or are without accessory tooth.

The characteristic gape in the chela of the major second pereiopod in *P. incertus* (fig. 16A, B) is also present in the new species. *Periclimenes incertus* is the only species in the *P. obscurus* species group associated with sponges. The original description by Borradaile (1915) is brief. Kemp (1922) described *Periclimens impar* based on a single ovigerous female collected from a sponge at Port Blair, Andaman Islands. Holthuis (1952) showed that the difference used by Kemp to separate *P. impar* from *P. incertus* is not correct and suggested that *P. impar* might be a junior synonym of *P. incertus*. Kemp (1922) separated *P. incertus* from *P. impar* by the fact that in *P. impar* at least one tooth of the dorsal series of the rostrum is placed on the carapace, while in *P. incertus* all teeth are situated on the rostrum proper. This does not hold as the type specimen figured by Borradaile (1917: pl. 53, fig. 7) shows a distinct tooth on the carapace. Holthuis (1959) was able to confirm this when he reexamined the type material of *P. incertus* in the collection of the University Museum of Zoology in Cambridge and synonymized *P. impar* with *P. incertus*. Specimens collected from a sponge host at Semporna, Sabah, Malaysia (figs. 8C, D, 15–17) and identified as *P. incertus* on the bases of the description by Kemp of *P. impar* were used for morphological and molecular comparisons. The specimens (fig. 8C, D) fit the colour description provided by Kemp (1922: 149): ‘The specimen was found on a sponge of pinkish colour and was transparent when alive with reddish patches on the

abdominal pleura’ and Bruce (1980: 13): ‘Highly transparent, with fine paired red striae along the lower branchiostegite and abdomen.’

The new species differs morphologically from *P. incertus* (figs. 15–17) in: 1) having the ventral margin of the rostrum slightly convex (fig. 10B) while it is straight in *P. incertus* (Fig. 15B); 2) in processing one subdistal tooth on the ventral lamina on the rostrum (fig. 10B) whereas *P. incertus* has one or two teeth there (fig. 15B); 3) in having the proximalmost tooth on the rostrum situated at the level of the orbit (fig. 10A), whereas in *P. incertus* it is demarcated from the dorsal carine, and situated behind the orbit on the carapace proper, at the level of the hepatic spine (fig. 15A); 4) in having the setal ridges on the basis and ischium of the first pereiopod moderately developed with few long simple setae (figs. 10G, 11C), whereas in *P. incertus* these ridges (fig. 15C, E, F) are more pronounced with more long simple setae; 5) in having the medial process on the coxa with few simple setae (fig. 10G), whereas in *P. incertus* this medial process (fig. 15E) has apart from the simple setae a very long robust seta overreaching the basis; 6) in having the fingers of the chela of the first pereiopod as long as the palm (fig. 10E), whereas in *P. incertus* the palm is distinctly longer than the fingers (fig. 15D); 7) in having the proximal cutting edge of the fingers of the chela of the second minor cheliped entire (fig. 12A), whereas in *P. incertus* small tubercles are present there (fig. 16D); 8) in having the fourth thoracic sternite with a medially notched median plate between the first pereiopods (fig. 10G), whereas this is not notched in *P. incertus* (fig. 15F); 9) in having the accessory tooth of the dactyli of the ambulatory pereiopods as robust as the unguis and slightly falling short of the unguis in length (fig. 13B, D, F), whereas in *P. incertus* the accessory tooth is more robust than the unguis and as long as the unguis (fig. 17A, B).

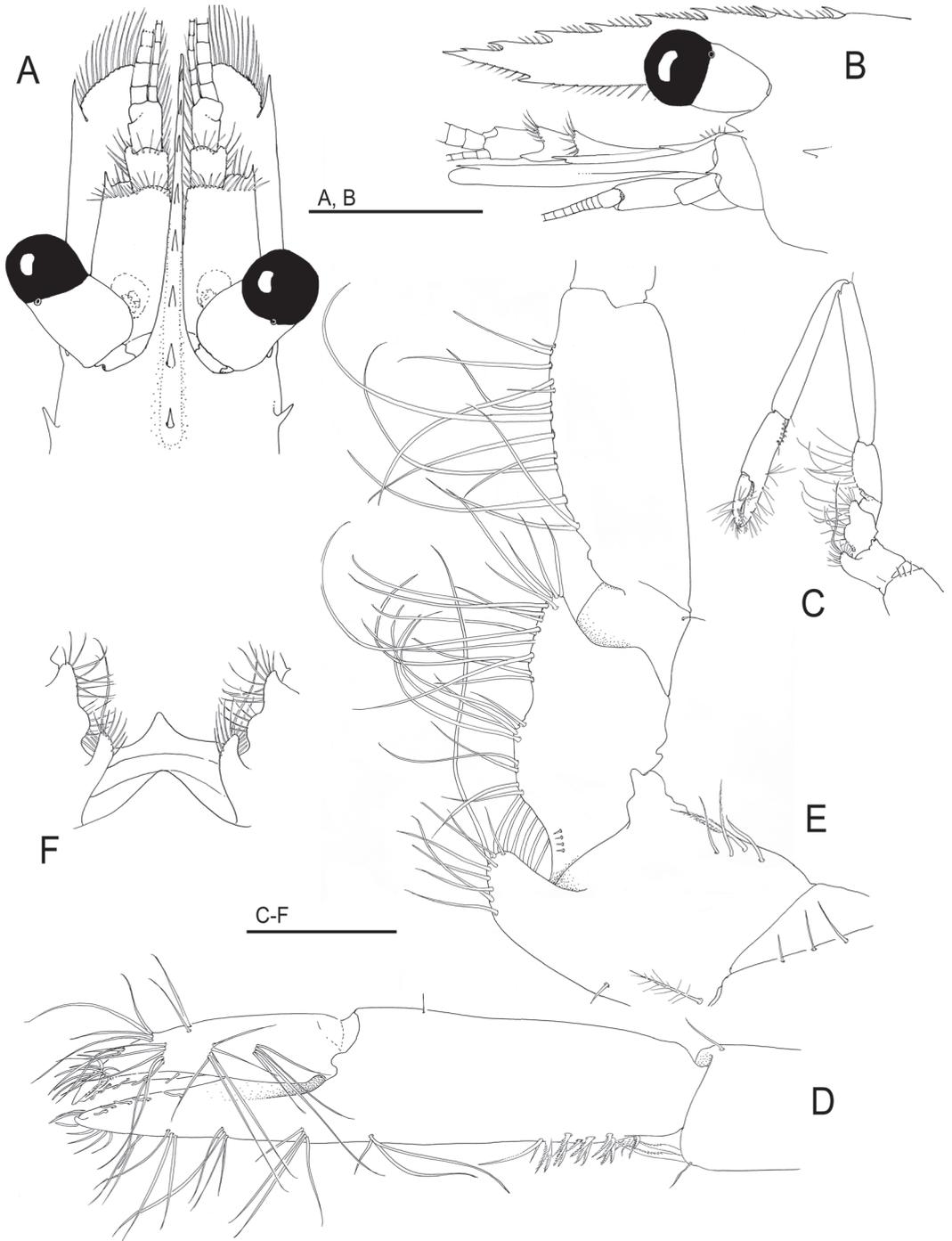


FIGURE 15 *Periclimenes incertus* Borradaile, 1915, ovigerous female, RMNH.CRUS.D.53946. A, rostrum and anterior appendages, dorsal view; B, idem, lateral view; C, left first pereiopod; D, idem, chela; E, idem, proximal segments; F, fourth thoracic sternites and proximal segments of first pereiopods. Scale bar: A–C = 1 mm; D–E = 0.2 mm; F = 0.4 mm.

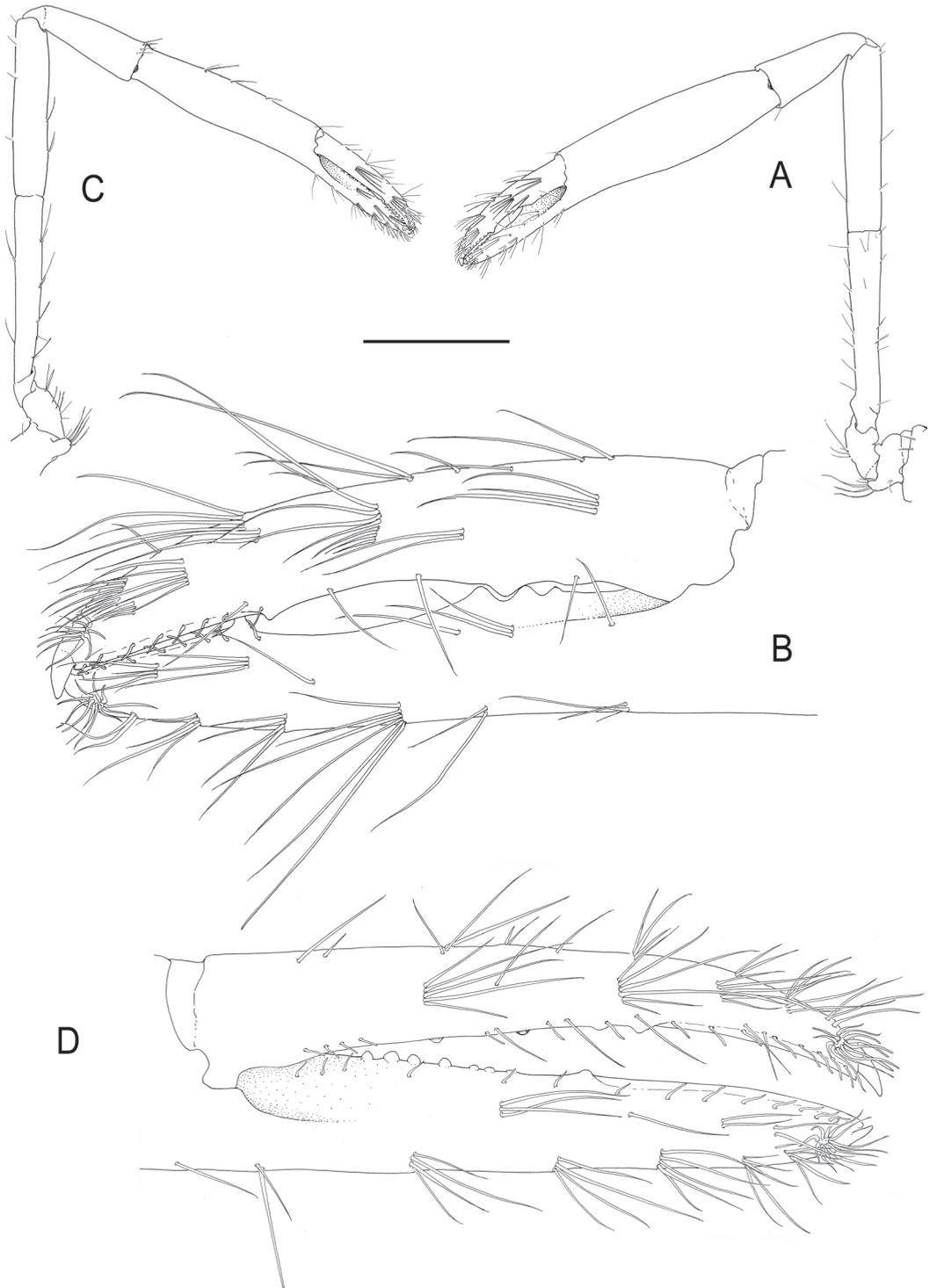


FIGURE 16 *Periclimenes incertus* Borradaile, 1915, ovigerous female, RMNH.CRUS.D.53946. A, left major second pereiopod; B, idem, chela; C, right minor second pereiopod; D, idem, chela. Scale bar: A, C = 1 mm; B, D = 0.2 mm.



FIGURE 17 *Periclimenes incertus* Borradaile, 1915, ovigerous female, RMNH.CRUS.D.53946. A, left third pereopod; B, idem dactylus. Scale bar: A = 1 mm; B = 0.2 mm.

The other closely related species is the black-coral-associated *Periclimenes zeviniae* Āuriš, 1990. *P. zeviniae* was described on the basis of a single female from the Maldives. As Āuriš (1990) suspects, the specimen is not an adult, which makes comparison with adult features of the other members of the species group difficult. However, this species is similar to the new species in many respects. With *P. incertus* and the new species it shares the ventrally denticulate ambulatory dactyli, a unique character within the *P. obscurus* group, as well as the robust accessory tooth of the ambulatory pereopods. *P. zeviniae* however, has the tips of the fingers of the chela of the first pereopods flattened, 'nail-like'. *P. zeviniae* is the only species in the *P. obscurus* group with this character. *P. subcorallum* sp. nov. has the fingers not flattened, nor 'nail-like'.

Fransen (1994) recorded specimens from the Seychelles with ventrally denticulate ambulatory dactyli which he thought to be

possibly conspecific with *P. zeviniae* Āuriš, 1990 as these specimens possess the 'nail-like' tips on the fingers of the first pereopods. These specimens are full grown and show some differences in the dentition of the rostrum and ornamentation of the chela of the second pereopods compared with the subadult holotype of *P. zeviniae*. With regards to the second pereopods these specimens show the same features as the *P. subcorallum* sp. nov. The rostrum however differs as an epigastal tooth is present which was not observed in *P. subcorallum* sp. nov.

4 Discussion

Three shrimp species of *Periclimenes* were found to live in association with mushroom corals of which one is new to science. Hoeksema et al. (2012) recorded 40 associations between mushroom corals and shrimp. This

study adds another 15 different pairs of shrimp and host coral species.

Although various species of scleractinians have been recorded as hosts for palaemonid shrimps, most mushroom coral species (about 80%) are different from other scleractinians because they are initially attached (Hoeksema & Yeemin, 2012) but free-living when they are full-grown (Hoeksema, 1989; Gittenberger et al., 2011; Benzoni et al., 2012). This implies that they can offer space to associated fauna underneath the corals, as seen in some gastropods (Gittenberger & Hoeksema, 2013), sessile ctenophores (Hoeksema et al., 2013b; Alamaru et al., 2016), brittle stars (Bos & Hoeksema, 2017), and shrimps (Hoeksema & Fransen, 2011; present study). Even large corallivorous snails can use the space underneath mushroom corals to hide themselves during daylight (Hoeksema et al., 2013a) and use this same space also to lay their eggs (Scott et al., 2017).

It is obvious that mushroom coral species with a large maximum size offer more shelter space than smaller species, while they usually also get a more convex growth form with additional room underneath (Hoeksema & Moka, 1989; Hoeksema, 1991, 1993). Among the host species recorded, none belong to the mushroom coral genus *Cycloseris*, which are usually relatively small with a smooth or flat underside or encrusting, offering little shelter space (Benzoni et al., 2012; Hoeksema, 2014). Corals of free-living *Cycloseris* species usually occur on soft substrates causing the risk of burial (Schuhmacher, 1977; Bongaerts et al., 2012), they may be able to fragment themselves (Hoeksema & Waheed, 2011, 2012) and move around (Hoeksema et al., 2012, 2018, 2019a, b), which is not a stable environment for shrimps and other animals that need to hide themselves underneath (Gittenberger & Hoeksema, 2013).

It is noteworthy that five small shrimp species of the genus *Periclimenes* show much overlap in their host choice (table 3) and that

these hosts belong to various coral genera that form a polyphyletic group within the family Fungiidae (Gittenberger et al., 2011). This indicates that host specificity among these shrimp species is predominantly determined at a high taxonomic level, as also seen in some other crustaceans, like gall crabs (Van der Meij et al., 2015) and copepods (Ivanenko et al., 2018).

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References

- Alamaru, A., Brokovich, E. & Loya, Y. (2016) Four new species and three new records of benthic ctenophores (Family: Coeloplanidae) from the Red Sea. *Mar. Biodivers.*, 46, 261–279.
- Balss, H. (1914) Über einige Pontoniiden. *Zool. Anz.*, 45, 83–88.

- Barnard, K.H. (1958) Further additions to the crustacean fauna-list of Portuguese East Africa. *Mem. Museu Dr. Alvaro de Castro*, 4, 3–23.
- Benzoni, F., Arrigoni, R., Stefani, F., Reijnen, B.T., Montano, S. & Hoeksema, B.W. (2012) Phylogenetic position and taxonomy of *Cycloseris explanulata* and *C. wellsii* (Scleractinia: Fungiidae): lost mushroom corals find their way home. *Contrib. Zool.*, 81, 125–146.
- Berggren, M. (1994) *Periclimenes nomadophila* and *Tuleariocaris sarec*, two new species of pontoniine shrimps (Decapoda: Pontoniinae), from Inhaca Island, Moçambique. *J. Crustacean Biol.*, 14, 782–802.
- Bongaerts, P., Hoeksema, B.W., Hay, K.B. & Hoegh-Guldberg, O. (2012) Mushroom corals overcome live burial through pulsed inflation. *Coral Reefs*, 31, 399.
- Borradaile, L.A. (1915) Notes on Carides. *Ann. Mag. Nat. Hist.*, 8, 205–213.
- Borradaile, L.A. (1917) The Percy Sladen Trust Expedition to the Indian Ocean in 1905, under the leadership of Mr. J. Stanley Gardiner, M.A. No. VIII. On the Pontoniinae. *Trans. Linn. Soc. London, Ser. 2, Zool.*, 17, 323–396.
- Bos, A.R. & Hoeksema, B.W. (2017) Mushroom corals (Fungiidae) in the Davao Gulf, Philippines, with records of associated fish and other cryptofauna. *Raffles Bull. Zool.*, 65, 198–206.
- Brinkmann, B.W. & Franssen, C.H.J.M. (2016) Identification of a new stony coral host for the anemone shrimp *Periclimenes rathbunae* Schmitt, 1924 with notes on the host-use pattern. *Contrib. Zool.*, 85, 437–456.
- Bruce, A.J. (1966) Note on some Indo-Pacific Pontoniinae. XI. A re-examination of *Philarius lophos* Barnard, with the designation of a new genus, *Ischnopontonia*. *Bull. Mar. Sci.*, 16, 584–598.
- Bruce, A.J. (1967) Notes on some Indo-Pacific Pontoniinae III–IX. Description of some new genera and species from the western Indian Ocean and the South China Sea. *Zool. Verh. Leiden*, 87, 1–73.
- Bruce, A.J. (1969) Preliminary descriptions of sixteen new species of of the genus *Periclimenes* Costa, 1844 (Crustacea, Decapoda, Natantia, Pontoniinae). *Zool. Meded. Leiden*, 43, 253–278.
- Bruce, A.J. (1970) Notes on some Indo-Pacific Pontoniinae. XV. *Hamopontonia corallicola* gen. nov., sp. nov. a new pontoniid shrimp from Hong Kong. *Crustaceana*, 18, 37–48.
- Bruce, A.J. (1973a) Notes on some Indo-Pacific Pontoniinae. XXII. *Pliopontonia furtiva* gen. nov., sp. nov., a new shrimp associated with a corallimorph zoantharian. *Crustaceana*, 24, 97–109.
- Bruce, A.J. (1973b) Notes on some Indo-Pacific Pontoniinae. XXIII. *Tectopontonia maziwiae* gen. nov., sp. nov., a new coral associate from Tangaynika (Decapoda, Palaemonidae). *Crustaceana*, 24, 169–180.
- Bruce, A.J. (1976a) A report on a small collection of shrimps from the Kenya National Marine Parks at Malindi, with notes on selected species. *Zool. Verh. Leiden*, 145, 1–72.
- Bruce, A.J. (1976b) A report on some pontoniid shrimps collected from the Seychelle Islands by the F.R.V. *Manihine*, 1972, with a review of the Seychelles pontoniid shrimp fauna. *Zool. J. Linn. Soc.*, 59, 89–153.
- Bruce, A.J. (1979) *Ctenopontonia cyphastreophila*, a new genus and species of coral associated pontoniine shrimp from Eniwetok Atoll. *Bull. Mar. Sci.*, 29, 423–435.
- Bruce, A.J. (1980) On some pontoniine shrimps from Noumea, New Caledonia. *Cah. l'Indo-Pac.*, 2, 1–39.
- Bruce, A.J. (1989) *Periclimenes goniopora* sp. nov. (Crustacea: Decapoda: Palaemonidae), a new coelenterate-associated shrimp. *Beagle Rec. Mus. Art Gall. North. Territ.*, 6, 149–156.
- Bruce, A.J. (1997) A new pontoniine shrimp genus (Crustacea: Decapoda) from the Yemen, with a note on other species. *J. Nat. Hist.*, 31, 1213–1222.
- Bruce, A.J. (1998) Pontoniine shrimps from Moreton Bay, Queensland (Crustacea: Decapoda, Pontoniinae). *Mem. Queensl. Mus.*, 42, 387–398.
- Bruce, A.J. (2007) Palaemonoid shrimps from the Dampier Archipelago (Crustacea: Decapoda),

- with a review of the Western Australian pontoniine shrimp fauna. *Rec. West. Aust. Mus.*, 73 (Suppl.), 97–129.
- Bruce, A.J. (2010) Pontoniine shrimps (Crustacea: Decapoda: Palaemonidae) from the CReefs 2009 Heron Island Expedition, with a review of the Heron island pontoniine fauna. *Zootaxa*, 2541, 50–68.
- Bruce, A.J. & Coombes, K.E. (1995) The palaemonoid shrimp fauna (Crustacea: Decapoda: Caridea) of the Cobourg Peninsula, Northern Territory. *Beagle Rec. Mus. Art Gall. North. Territ.*, 12, 101–144.
- Clark, A.H. (1919) Some necessary changes in crustacean nomenclature. *Proc. Biol. Soc. Wash.*, 32, 199.
- Costa, O.G. (1844) Su due nuovi generi di Crostacei decapodi macrouri. *Ann. Accad. Aspir. Nat. Napoli*, 2, 285–292.
- Dana, J.D. (1846) United States Exploring Expedition during the years 1838–1842. *Zoophytes*, 7, 1–740. Lea and Blanchard, Philadelphia.
- Dana, J.D. (1852) Conspectus Crustaceorum, quae in Orbis Terrarum circumnavigatione, Carolo Wilkese Classe Republicae Foederatae Duce, lexit et descripsit. *Proc. Acad. Nat. Sci. Phil.*, 1852, 10–28.
- De Grave, S. (1998) Pontoniinae (Decapoda, Caridea) associated with *Heliofungia actiniformis* (Scleractinia) from Hansa Bay, Papua New Guinea. *Belg. J. Zool.*, 128, 13–22.
- De Grave, S. (2000) Caridean shrimps (Crustacea, Decapoda) from Hansa Bay, Papua New Guinea: Palaemonidae and Gnathophyllidae. *Bull. K. Belg. Inst. Natuurw. Biol.*, 70, 119–148.
- De Grave, S. & Franssen, C.H.J.M. (2011) Carideorum catalogus: the Recent species of the dendrobranchiate, stenopodidean, procarididean and caridean shrimps (Crustacea: Decapoda). *Zool. Meded. Leiden*, 85, 195–589.
- Đuriš, Z. (1990) Two new species of the palaemonid shrimp genus *Periclimenes* from the Maldivian waters (Crustacea, Decapoda, Palaemonidae). *Acta Soc. Zool. Bohemoslovaca*, 54, 1–8.
- Đuriš, Z. & Lin, C.W. (2016) The ‘scorpion shrimp’, a new species of the genus *Metapontonia* (Crustacea: Decapoda: Palaemonidae) from Taiwan, with new generic record from Papua New Guinea. *Zootaxa*, 4138, 474–490.
- Eilbracht J. & Franssen, C.H.J.M. (2015) *Periclimenes macrorhynchia* sp. nov., a new hydrozoan-associated pontoniine shrimp (Crustacea, Decapoda, Palaemonidae) from North East Kalimantan, Indonesia. *Zootaxa*, 3994, 377–395.
- Esper, E.J.C. (1797) *Fortsetzungen der Pflanzenthier in Abbildungennach der Natur mit Farben erleuchtet nebst Beschreibungen. Erster Theil*. Nürnberg, pp. 1–230.
- Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. *Mol. Mar. Biol. Biotechnol.*, 3, 294–299.
- Franssen, C.H.J.M. (1989) Notes on caridean shrimps collected during the Snellius-II Expedition. I. Associates of Anthozoa. *Neth. J. Sea Res.*, 23, 131–147.
- Franssen, C.H.J.M. (1994) Marine palaemonoid shrimps of the Netherlands Seychelles Expedition 1992–1993. *Zool. Verh. Leiden*, 297, 85–152.
- Franssen, C.H.J.M. (1997) Indonesian pontoniine shrimps. In: T. Tomascik, A.J. Mah, A. Nontji & M. Kasim Moosa (Eds), *The Ecology of the Indonesian Seas, Part II, Box 21.3*, pp. 1064–1075.
- Franssen, C.H.J.M. & Holthuis, L.B. (2007) *Virsmi* spec. nov., a new scleractinian associated pontoniine shrimp (Crustacea: Decapoda: Palaemonidae) from the Indo-West Pacific. *Zool. Meded. Leiden*, 81, 101–114.
- Franssen, C.H.J.M. & Rauch, C. (2013) *Hamodactylus macrophthalmus* spec. nov., a new coral-associated pontoniine shrimp (Decapoda, Caridea, Palaemonidae) from Indonesia. *Zootaxa*, 3635, 286–296.
- Gittenberger, A. & Hoeksema, B.W. (2013) Habitat preferences of coral associated wentletrap snails (Gastropoda: Epitoniidae). *Contrib. Zool.*, 82, 1–25.

- Gittenberger, A., Reijnen, B.T. & Hoeksema, B.W. (2011) A molecularly based phylogeny reconstruction of mushroom corals (Scleractinia: Fungiidae) with taxonomic consequences and evolutionary implications for life history traits. *Contrib. Zool.*, 80, 107–132.
- Hall, T.A. (2001) Bioedit: A User-Friendly Biological Sequence Alignment Editor and Analysis, version 5.09. Department of Microbiology, North Carolina State University, North Carolina.
- Hoeksema, B.W. (1989) Taxonomy, phylogeny and biogeography of mushroom corals (Scleractinia: Fungiidae). *Zool. Verh. Leiden*, 254, 1–295.
- Hoeksema, B.W. (1991) Evolution of body size in mushroom corals (Scleractinia: Fungiidae) and its ecomorphological consequences. *Neth. J. Zool.*, 41, 122–139.
- Hoeksema, B.W. (1993) Phenotypic corallum variability in Recent mobile reef corals. *Cour. Forsch.-Inst. Senckenb.*, 164, 263–272.
- Hoeksema, B.W. (2012) Evolutionary trends in on-shore-offshore distribution patterns of mushroom coral species (Scleractinia: Fungiidae). *Contrib. Zool.*, 81, 199–221.
- Hoeksema, B.W. (2014) The “*Fungia patella* group” (Scleractinia, Fungiidae) revisited with a description of the mini mushroom coral *Cycloseris boschmai* sp. n. *ZooKeys*, 371, 57–84.
- Hoeksema, B.W. (2017) The hidden biodiversity of tropical coral reefs. *Biodiversity*, 18, 8–12.
- Hoeksema, B.W. & Franssen, C.H.J.M. (2011) Space partitioning by symbiotic shrimp species co-habiting in the mushroom coral *Heliofungia actiniformis* at Semporna, eastern Sabah. *Coral Reefs*, 30, 519.
- Hoeksema, B.W. & Moka, W. (1989) Species assemblages and ecomorph variation of mushroom corals (Scleractinia: Fungiidae) related to reef habitats in the Flores Sea. *Neth. J. Sea Res.*, 23, 149–160.
- Hoeksema, B.W. & Waheed, Z. (2011) Initial phase of autotomy in fragmenting *Cycloseris* corals at Semporna, eastern Sabah, Malaysia. *Coral Reefs*, 30, 1087.
- Hoeksema, B.W. & Waheed, Z. (2012) Onset of autotomy in an attached *Cycloseris* coral. *Galaxea J. Coral Reef Stud.*, 14, 1–2.
- Hoeksema, B.W. & Yeemin, T. (2011) Late detachment conceals serial budding by the free-living coral *Fungia fungites* in the Inner Gulf of Thailand. *Coral Reefs*, 30, 975.
- Hoeksema, B.W., van der Meij, S.E.T. & Franssen, C.H.J.M. (2012) The mushroom coral as a habitat. *J. Mar. Biol. Assoc. U.K.*, 92, 647–663.
- Hoeksema, B.W., Scott, C. & True, J.D. (2013a) Dietary shift in corallivorous *Drupella* snails following a major bleaching event at Koh Tao, Gulf of Thailand. *Coral Reefs*, 32, 423–428.
- Hoeksema, B.W., Waheed, Z. & Alamaru, A. (2013b) Out of sight: aggregations of epizoic comb jellies underneath mushroom corals. *Coral Reefs*, 32, 1065.
- Hoeksema, B.W., Bouwmeester, J., Range, P. & Ben-Hamadou, R. (2018) A large aggregation of self-fragmenting mushroom corals in the Arabian / Persian Gulf. *Ecology*, 99, 1236–1238.
- Hoeksema, B.W., Sellanes, J. & Easton, E.E. (2019a) A high-latitude, mesophotic *Cycloseris* field at 85 m depth off Rapa Nui (Easter Island). *Bull. Mar. Sci.*, 95, 101–102.
- Hoeksema, B.W., Giyanto & Suharsono (2019b) The role of maximum shelf depth versus distance from shore in explaining a diversity gradient of mushroom corals (Fungiidae) off Jakarta. *Diversity*, 11, 46.
- Holthuis, L.B. (1951) A general revision of the Palaemonidae (Crustacea, Decapoda Natantia) of the Americas. I. The subfamilies Euryrhynchiinae and Pontoniinae. *Occas. Pap. Allan Hancock Found.*, 11, 1–332.
- Holthuis, L.B. (1952) The Decapoda of the *Siboga* Expedition. Part XI. The Palaemonidae collected by the *Siboga* and *Snellius* Expeditions with remarks on other species. II. Subfamily Pontoniinae. *Siboga Exped. Monogr.*, 39a 10, 1–252.
- Holthuis, L.B. (1959) Results of the reexamination of the type specimens of some species belonging to the subfamilies Pontoniinae and

- Palaemoninae (Crustacea Decapoda Macrura). *Zool. Meded. Leiden*, 36, 193–200.
- Horká, I., De Grave, S., Franssen, C.H.J.M., Petrusek, A. & Ďuriš, Z. (2016) Multiple host switching events shape the evolution of symbiotic palaemonid shrimps (Crustacea: Decapoda). *Sci. Rep.*, 6, 26486.
- Ivanenko, V.N., Hoeksema, B.W., Mudrova, S.V., Nikitin, M.A., Martínez, A., Rinskaya-Korsakova, N.N., Berumen, M.L. & Fontaneto, D. (2018) Lack of host specificity of copepod crustaceans associated with mushroom corals in the Red Sea. *Mol. Phylogenet. Evol.*, 127, 770–780.
- Jukes, T.H. & Cantor, C.R. (1969) *Evolution of Protein Molecules*. Academic Press, New York, pp. 21–132.
- Kemp, S. (1922) Notes on Crustacea Decapoda in the Indian Museum, 15. Pontoniinae. *Rec. Ind. Mus.*, 24, 113–228.
- Klunzinger, C.B. (1879) *Die Korallenthiere des Rothen Meeres, 3. Theil: Die Steinkorallen. Zweiter Abschnitt: Die Asteraeaceen und Fungiaceen*. Gutmann, Berlin, pp. 1–100.
- Lamarck, J.B. (1801) *Système des animaux sans vertèbres, ou tableau général des classes, des ordres et des genres de ces animaux; Présentant leurs caractères essentiels et leur distribution, d'après la considération de leurs rapports naturels et de leur organisation, et suivant l'arrangement établi dans les galeries du Muséum d'Histoire Naturelle, parmi leurs dépouilles conservées; Précédé du discours d'ouverture du Cours de Zoologie, donné dans le Muséum National d'Histoire Naturelle l'an 8 de la République*. Published by the author and Deterville, Paris, viii + 432 pp.
- Linnaeus, C. (1758) *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata*. Laurentius Salvius, Holmiae, ii, 824 pp.
- Meij, S.E.T. van der, Franssen, C.H.J.M., Pasman, L.R. & Hoeksema, B.W. (2015) Phylogenetic ecology of gall crabs (Cryptochiridae) as associates of mushroom corals (Fungiidae). *Ecol. Evol.*, 5, 5770–5780.
- Nemenzo, F. (1955) Systematic studies on Philippine shallow water scleractinians: I. Suborder Fungiida. *Nat. Appl. Sci. Bull. Univ. Philipp.*, 15, 3–84.
- Okuno, J. (1999) *Izocaris masudai*, new genus, new species (Decapoda: Caridea: Palaemonidae), a sea anemone associate from Japan. *J. Crustacean Biol.*, 19, 397–407.
- Okuno, J. (2009) *Pliopontonia harazakii* sp. nov., a new species of coral-associated shrimp (Decapoda: Caridea: Palaemonidae) from Yaku-shima Island, southern Japan. *Bulletin of the National Museum of Nature and Science (A, Zoology), Suppl.*, 3, 105–113.
- Okuno, J. & Bruce, A.J. (2010) Designation of *Ancylomenes* gen. nov., for the 'Periclimenes species group' (Crustacea: Decapoda: Palaemonidae), with the description of a new species and a checklist of congeneric species. In: S. De Grave & C.H.J.M. Franssen (Eds), *Contributions to shrimp taxonomy. Zootaxa*, 2372, 85–105.
- Pallas, P.S. (1766) *Elenchus zoophytorum sistens generum adumbrationes generaliores et specierum cognitarum succinctas descriptiones, cum selectis auctorum synonymis*. Fransiscum Varrentrapp, Hagae, 451 pp.
- Posada, D. (2008) jModelTest: Phylogenetic model averaging. *Mol. Biol. Evol.*, 25, 1253–1256.
- Quelch, J.J. (1886) Report on the Reef-corals collected by H.M.S. 'Challenger' during the years 1873–76. *Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873–1876. Zoology*, 16 (part 46), 1–203.
- Quoy, J.R.C. & Gaimard, J.P. (1833) *Zoologie IV: Zoophytes. In: Zoologie. Voyage de la corvette l'Astrolabe: exécuté par ordre du roi, pendant les années 1826–1827–1828–1829 / sous le commandement de J. Dumont d'Urville*. J. Tastu, Paris, pp. 1–390.
- Rafinesque, C.S. (1815) *Analyse de la Nature ou Tableau de l'Univers et des corps organisés*. Palerme, pp. 1–224.
- Schenkel, E. (1902) Beitrag zur Kenntniss der Dekapodenfauna von Celebes. *Verhandlungen der Naturforschenden Gesellschaft in Basel*, 13, 485–585.

- Schuhmacher, H. (1977) Ability in fungiid corals to overcome sedimentation. *Proc. 3rd Int. Coral Reef Symp.*, 1, 503–509.
- Scott, C.M., Mehrotra, R. & Hoeksema, B.W. (2017) *In-situ* egg deposition by corallivorous snails on mushroom corals at Koh Tao (Gulf of Thailand). *J. Mollusc. Stud.*, 83, 360–362.
- Stimpson, W. (1860) *Prodomus descriptionis animalium everttevratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, C. Ringgold et J. Rodgers Ducibus, observavit et descripsit. Proc. Acad. Nat. Sci. Phil.*, 1860, 22–47.
- Swofford, D.L. (2003) *PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods)*. Version 4. Sinauer Associates, Sunderland, MA.
- Thompson, J.D., Higgins, D.G. & Gibson, T.J. (1994) CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Res.*, 22, 4673–4680.
- Verrill, A.E. (1864) List of the polyps and corals sent by the Museum of Comparative Zoology to other institutions in exchange, with annotations. *Bull. Mus. Comp. Zool.*, 1, 29–60.

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